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Using stable isotope analysis to estimate black bear (Ursus americanus) diet in Vermont

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USING STABLE ISOTOPE ANALYSIS TO ESTIMATE BLACK BEAR (*URSUS AMERICANUS*) DIET IN VERMONT

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ABSTRACT

The black bear (*Ursus americanus*) is an iconic species with cultural, economic and ecological importance in Vermont, USA. Bears exhibit a highly variable diet, and few studies have described bear diet in the state. Information on diet may provide insight into foraging behavior, thus allowing managers to better assess patterns of human-bear conflict. My objectives were to estimate the relative contribution of food items to bear diet and how factors including sex, habitat, food availability, and nuisance status describe patterns of consumption. I collected samples from bears and major food groups including C_3 plants, white-tailed deer (*Odocoileus virginianus*), corn (*Zea mays*), and human foods, then quantified diet using stable isotope analysis. Samples were collected from 71 bears, 547 plants, and 38 deer throughout Vermont. I also collected 12 corn samples, and 20 human hair samples to represent anthropogenic foods. I determined $\delta^{13}C$ and $\delta^{15}N$ isotope values for all samples, then used Bayesian mixing models to estimate the contribution of foods and effect of each factor on proportional contribution estimates. Nuisance status best described patterns of diet over other factors. Median percent contributions for non-nuisance bears were 73.2% C_3 plants, 23.8% corn, 1.9% human foods, and 0.5% deer. Median percent contributions for nuisance bears were 64.6% C_3 plants, 28.9% corn, 3.2% human foods, and 0.7% deer. Factors such as sex, habitat, and food availability exerted less effect on diet than expected. Proportional contribution of meat was lower than in some other parts of North America, suggesting bears forage differently in Vermont. Results provide the first statewide estimate of bear diet and indicate corn may represent a much larger component of diet than previously thought. In particular, bears labeled as nuisance animals may forage on greater proportions of corn throughout the year.

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CHAPTER 1: INTRODUCTION

1.1 Overview of Research

As opportunistic omnivores, black bears (*Ursus americanus*) are known to take advantage of anthropogenic foods to some extent; a behavior that can lead to food-conditioning and human-bear conflict. Despite the importance of black bears as a managed furbearer, bear diet has not been comprehensively studied. A greater understanding of black bear diet composition may reveal the extent of anthropogenic foraging within the Vermont bear population. Understanding which factors influence proportional contribution of food items to black bear diet (e.g. natural foods and anthropogenic foods) may provide insight for black bear management decisions.

This research used stable isotope analysis to analyze proportional contribution of food items to black bear diet in Vermont, and examined the factor(s) that may influence diet differences within the population. Used in combination with other methods of diet analysis, the results will contribute to the management of the species in Vermont.

1.2 Overview of Chapters

The thesis is comprised of four chapters:

1) A review of relevant literature on the topics of: black bear ecology, human-wildlife conflict, stable isotope analysis and Bayesian mixing models;
2) A scientific article written for publication detailing the results of the study;
3) A comprehensive bibliography;
4) Appendices.

CHAPTER 2: LITERATURE REVIEW

2.1 Black Bear Ecology

2.1.1 Importance of the black bear

The black bear (*Ursus americanus*) represents an iconic symbol of wilderness (Kellert 1994). The species also plays important ecological roles, including acting as a long-distance seed disperser (Auger et al. 2002) and conservation roles such as serving as an umbrella species due to its dependence on forest habitat connectivity (Lambeck 1997). Black bears also have economic value as a game species, hold symbolic and traditional value, and are generally perceived in a highly positive manner by most North Americans; although negative attitudes expressed by some groups such as livestock producers may be common (Kellert 1994).

2.1.2 Black bear status in Vermont

Native to Vermont, the black bear is found primarily in remote forested habitat throughout the state (Hammond 2002). Areas of greatest population density include the Green Mountains, and northeastern counties of Orleans, Caledonia, and Essex (Willey 1978). Historically, black bears were confined to forested mountain areas, largely as a result of initial human settlement and deforestation for agriculture (Foster et al. 2002). As forest returned to Vermont beginning in the late 19th century and early 20th century, the bear population increased (Haskell et al. 2010). Today, bears occur in approximately 80% of Vermont (Haskell et al. 2010) and the population is estimated at or over the Big Game Management Plan population objective of 4,500 to 6,000 individuals (Kart et al. 2005; Vermont Fish and Wildlife Department 2011). Although population regulation

through harvest has been in practice for much longer, in the 1980s the Vermont Fish and Wildlife Department began managing black bears through habitat conservation (Hammond 2002). The Vermont Wildlife Action Plan identified habitat loss due to fragmentation and development as the largest risk to critical black bear habitat (such as mast stands, travel corridors and wetlands) (Kart et al. 2005). Black bears are dependent on large forested habitat, habitat mosaics and connectivity of habitat to provide adequate food supplies (Kart et al. 2005). Black bear occupancy probability in Vermont has been found to be positively associated with percent forest and negatively associated with percent human development within 5 km of a given location (Long et al. 2011).

2.1.3 Feeding ecology

Throughout their native range, black bears exhibit an omnivorous diet, a majority of which is comprised of vegetation (Larivière 2001). In the spring, black bears in the northeast feed primarily on green vegetation, and, in years following good fall mast crops, overwintered hard mast (McDonald and Fuller 2005). During this season, black bears also opportunistically feed on neonate ungulates while traveling between vegetation-rich patches (Bastille-Rousseau et al. 2011). In Vermont, Willey (1978) reported spring diet to include sedges, grasses, herbs, horsetail (*Equisetum* spp.), oak (*Quercus* spp.) acorns, American beech (*Fagus grandifolia*) nuts, evergreen needles, roots, buds and carrion. Summer diet consists of soft mast such as berries, insects, herbaceous vegetation and Jack-in-the-pulpit corms (*Arisaema triphyllum*), whereas fall diet is comprised mainly of hard mast and fruit including blackberries (*Rubus* spp.), apples (*Malus* spp.), cherries (*Prunus* spp.), acorns and beech nuts (Willey 1978).

A scat analysis study on Stratton Mountain in Vermont resulted in a comprehensive list of plant and animal species consumed by black bears. Three species of plant were found to be consistently consumed during the spring, summer and fall including: tall nodding sedge (*Carex gynandra*), which was consumed mainly in the early spring, Jack-in-the-pulpit (*Arisaema triphyllum*) root corms, and jewelweed (*Impatiens capensis*) (Hammond 2002). Late summer and fall foods consumed when available consisted of American beech (*Fagus grandifolia*) nuts, apples (*Malus* spp.), oak (*Quercus* spp.) acorns, black cherry (*Prunus serotina*), choke cherry (*P. virginiana*), raspberries (*Rubus* spp.), blackberries (*Rubus* spp.), mountain ash (*Sorbus americana*) berries, blueberries (*Vaccinium* spp.), shadbush (*Amalanchier* spp.) berries and corn (*Zea mays*) among other sources (Hammond 2002). Skunk cabbage (*Sympolocarpus foedidus*) and squaw root (*Conopholis americana*) are important food sources to bears in Massachusetts and New Hampshire but are almost nonexistent in Vermont's bear habitat (Hammond 2002).

Black bears rely on widely fluctuating food sources that impact reproductive success, recruitment, mortality rates, movements and nuisance behavior (Elowe and Dodge 1989; Garshelis and Pelton 1981; Hammond 2002; McLaughlin et al. 1994). Following emergence from dens in early spring, bears experience a time of nutritional stress and have high fiber diets. Late spring through early fall diets are high in protein. High-energy late fall diets provide bears with the fats and carbohydrates necessary to increase body weight and energy storage in preparation for the winter metabolism (Beeman and Pelton 1980; Eagle and Pelton 1983; Elowe and Dodge 1989). Availability of fall foods rich in fats and carbohydrates such as acorns and beech nuts is thought to be

critical to reproductive success, dispersal and bear survival (Beeman and Pelton 1980; McLaughlin et al. 1994). Abundance of fall mast crops has been found to influence reproductive success in the following winter, with greater success following good mast years (Elowe and Dodge 1989). In Maine, bear reproductive synchrony in relation to abundance of beech nuts has been well documented (McLaughlin et al. 1994). This is supported by research showing that fall habitat use appears to be strongly governed by hard mast resource availability (Clark et al. 1994).

Although black bears can travel over large distances, they tend to confine their activities to areas known as home ranges. A home range is commonly defined as the area in which an animal conducts normal activities such as food gathering, breeding and rearing of young (Burt 1943). A territory, by comparison, is an area that is actively defended (Tinbergen 1957). In Vermont, male black bears have been found to have home ranges exceeding 100 km^2 whereas females have smaller home ranges around one third the size of male home ranges (Hammond 2002). In years when bears did not leave home ranges due to fall food scarcity, Hammond (2002) found that adult females had a mean home range size of 36.2 km^2 while adult males had a mean home range size of 158.2 km^2. The overall availability of food influences the selection and size of home range and territory (Amstrup and Beecham 1976). Although the influence of food productivity on black bear territoriality has not been adequately studied (Powell 1987), there is evidence to suggest that food is an important resource for black bears (Costello 2010; Powell et al. 1996).

Levels of food productivity may determine home range size and habitat selection seasonally as black bears will travel long distances to satisfy nutritional needs,

particularly when food items are scarce (Clark et al. 1994; Garshelis and Pelton 1981; Larivière 2001). In years of mast abundance, black bears in Vermont have been found at higher elevations, further from houses and roads than in other years. However, black bears will often travel outside of home ranges when fall food sources are scarce (Hammond 2002). In years when mast crops are poor, some black bears move to agricultural areas and feed on corn crops, at times traveling extensively to reach this anthropogenic food source (Elowe and Dodge 1989; McLaughlin et al. 1994). In poor mast years, bears feeding heavily in corn fields are better able to gain weight for winter survival than bears relying on natural foods (McDonald and Fuller 2001), in turn reducing the impact that a poor mast crop would otherwise have on litter production (McLaughlin et al. 1994). Garbage is another high calorie, highly valuable and often prolific food source for bears that improves body condition and fitness (Badyaev 1998). Anthropogenic foods are thought to be a significant contributor to the diet of some black bears in a population, but do not comprise a substantial percentage of the diet of the majority of black bears (Beeman and Pelton 1980). At least one study found that garbage was not a significant food source for bears (Merkle et al. 2011). However, few studies have examined the relative contribution of human foods to black bear diet, especially in the northeastern United States.

2.2 Human-Wildlife Conflict

2.2.1 Conflict overview

Human-bear conflict is increasing in both magnitude and frequency throughout the species range (Gore et al. 2006). Negative interactions between humans and bears

have the potential to diminish public acceptance of bear presence and lessen support for bear conservation programs, thereby making human-bear conflict reduction an important part of black bear management (Siemer and Decker 2010). In response to increases in reported human-bear conflicts, wildlife management organizations are reviewing management plans, increasing personnel hours spent on bear management and funding research and education programs intended to minimize conflict (Merkle et al. 2011). In practice, aspects of human-bear conflict management have the potential to draw resources away from other wildlife programs and injure the credibility of management agencies when controversial management such as nuisance animal destruction occurs (Hristienko and McDonald 2007). Efforts to reduce conflict, therefore, aim to preserve human safety, avoid controversial management (Hristienko and McDonald 2007), and protect black bears (Merkle et al. 2011). Research aimed at improving understanding of human-wildlife interactions has the potential to inform management decisions and reduce negative impacts. Knowledge gained is used to advise wildlife management decisions and public outreach programs aimed at minimizing negative wildlife impacts and maximizing benefits of wildlife presence in proximity to humans (Siemer and Decker 2010).

Processes of conditioning and habituation in both humans and wildlife can threaten human health and safety. Bears that suppress their reaction in a neutral situation involving people or display no overt reaction at all (Herrero et al. 2005) are considered habituated if this behavior is a result of repeated experience with anthropogenic stimuli (e.g. human scent, human development, humans) without consequence (Hopkins et al. 2010). Habituation is not to be confused with tolerance. A bear displaying tolerance to

humans may behave similarly to a habituated bear, but this behavior is not the result of learning (Hopkins et al. 2010). Habituation can be categorized as bear-to-bear habituation, bear-to-human habituation and human-to-bear habituation (Herrero et al. 2005; Hopkins et al. 2010; Smith et al. 2005). To the extent that the benefits of not reacting outweigh the perceived risks, habituation of bears to other bears and people will continue to occur (Herrero et al. 2005). Not only do many species of wildlife become habituated to the sights and sounds of human activity, but humans have equal potential to become habituated to wildlife (Siemer and Decker 2010). As a result of bears not behaving aggressively in the presence of humans, people become increasingly casual around bears (Hopkins et al. 2010). Additionally, humans may learn that by displaying nonthreatening behavior and/or food resources to wildlife, they receive unique viewing rewards (Siemer and Decker 2010). Because habituated bears and people learn to accept each other at closer distances, interactions are more probable (Herrero et al. 2005). Although the relationship between the complex behavioral concepts of habituation and food-conditioning is not fully understood (Herrero et al. 2005; Hopkins et al. 2010; Smith et al. 2005), black bears may be habituated but not food-conditioned, food-conditioned but not habituated, or habituated and food-conditioned (Hopkins et al. 2010). Human food conditioning may lead to habituation due to repeated exposure during foraging, and habituation can lead to opportunities for bears to positively associate humans with food rewards (Hopkins et al. 2010).

Wildlife professionals generally conclude that the solution to human-bear conflict is reducing availability of anthropogenic food sources (Gore and Knuth 2006) such as birdseed, garbage, compost, unattended grills, agricultural crops and outdoor pet food.

Focusing on changing human behavior, instead of controlling black bears, through required bear-proof storage containers, intensive education, regulation and enforcement has been identified as the most viable solution to human-bear conflict (Beckmann 2009). An important first-step in Vermont is to understand the extent of human food consumption by bears.

2.2.2 Food conditioning and anthropogenic food exploitation

Bears are opportunistic omnivores that may alter their natural behavior to benefit from easily accessed, high value food sources (Teunissen Van Manen 2011). Black bears demonstrate substantial tolerance for human presence and are often perceived as a nuisance species due to their consumption of human foods such as garbage, bird seed and agricultural crops (Herrero 2002). During years of poor natural food crops, black bears may seek out anthropogenic food sources (Noyce and Garshelis 1997). However, use of human foods is dependent on availability of nearby refuge habitat, regardless of how important the food source is to a bear population (Mattson 1990). Due to high caloric value and high relative availability (especially in urban areas) garbage is often cited as a major source of anthropogenic food for black bears leading to changes in activity patterns, behavior, shifts in distribution (Beckmann and Berger 2003b) and human-bear conflict (Beckmann and Berger 2003a). In some areas, fruit trees may be the most important attractant for black bears (Merkle et al. 2013).

Food rewards obtained in anthropogenic locations reinforce behavioral attraction to human food sources in a process known as food conditioning (Siemer and Decker 2010). A bear that has learned to associate the smell of people, presence of people,

human-use areas or food storage areas with food rewards is considered food-conditioned (Herrero et al. 2005). The level of food-conditioning varies between individuals and may be associated with factors such as natural tolerance of humans (Herrero et al. 2005; Smith et al. 2005), natural food availability, age class (Mattson 1990), anthropogenic food availability, and sex (Merkle et al. 2013). Food conditioning of black bears is considered to be the leading cause of human-bear conflict, and altering human behavior by reducing availability of human foods to bears is considered to be the best action for reducing human-bear conflict (Herrero 2002). Increased mortality rates and physiological and behavioral changes are experienced by food-conditioned black bears (Beckmann 2009). Not only do food-conditioned bears pose a safety risk for humans, but this type of habituation often causes expensive annual damage to cars, campsites, homes, livestock, crops and bee hives (Beckmann 2009). Decisions to relocate, aversely condition or use lethal control on bears that are food conditioned are difficult for managers with limited budgets and varied stakeholder groups to consider (Merkle et al. 2011).

Historically, humans have been responsible for encouraging food-conditioning of bears in the form of scheduled daily feedings. Park rangers in the early years of national parks fed bears garbage to provide the public with an opportunity to view wildlife up close (Zardus and Parsons 1980). Today, low visitor compliance to regulations surrounding intentional feeding and improper food storage in addition to increasing bear and human numbers continue to result in incidents between bears and humans in recreational areas (Teunissen Van Manen 2011). This is also true in residential areas, where homeowners may believe that bear visits are one-time events and often find it

unnecessary to reduce use of birdseed or cover garbage containers (Siemer and Decker 2010).

2.2.3 Habitat loss and fragmentation

Urban and suburban growth has resulted in a worldwide increase in human-wildlife interactions (Rosell and Llimona 2012). This increase in interactions is likely the result of human-induced redistribution of wildlife at a landscape level, rather than the result of increased wildlife populations (Beckmann and Berger 2003b). In the northeastern United States, unregulated hunting and habitat destruction for human land use resulted in a near eradication of black bears (Hammond 2002). Current populations are densest in areas with large unbroken forest tracts such as much of Maine, northern New Hampshire and northern Vermont (Hammond 2002). Today, the largest threat to black bears is human alteration and disturbance of wildland systems occupied by bears, specifically habitat destruction and disruption of spatiotemporal patterns of natural food production (Mattson 1990). Increased human alteration of bear habitat will influence populations, and most likely lead to greater levels of isolation that may have demographic and genetic consequences (Mattson 1990). Development of human structures such as roads have the potential to limit access to natural foods (Reynolds-Hogland and Mitchell 2007). In a fragmented landscape, areas of highly connected forests of a variety of types and forests nearby to agriculture are most important to black bears, suggesting use of agricultural crops in the absence of natural foods (Kindall and Manen 2007). As urbanization continues to encroach on remaining bear habitat, resulting habituation and

decreases in natural food availability are likely to cause an increase in human-bear conflict (Mattson 1990).

2.2.4 Conflict in Vermont

In a 2006 survey of North American wildlife management agencies in states with self-sustaining black bear populations, 82% of respondents reported that black bear related problems were common, increasingly common or a serious problem (Spencer et al. 2007). The majority of agencies (69%) indicated that garbage/food attractants were the most commonly reported type of human-bear conflict, followed by black bear sightings (Spencer et al. 2007). In the northeast, summer and spring are when the majority of reported conflict occurs (Spencer et al. 2007). Out of 39 states with substantial black bear populations, Vermont ranks 9th in number of complaints per 10,000 people (Spencer et al. 2007).

In Vermont, black bears have historically been confined to the forested spine of the Green Mountains. However, recent growth in the bear population combined with an increasing level of land development and fragmentation have resulted in a higher occurrence of bears within developed areas (Haskell et al. 2010). Widespread forest regeneration following farm abandonment in the late 1880s in addition to a change in cultural values and hunting regulations is likely responsible for Vermont's thriving bear population (Foster et al. 2002). Land-use legacies and disease have severely reduced the quantity of beech trees in Vermont forests compared to pre-settlement forests (Faison and Houston 2004). As evidenced by increasing numbers of bears in suburban areas (Foster et al. 2002; Reidel 2003), anthropogenic food is an attractive diet supplement that may

increase an area's carrying capacity for bears (Faison and Houston 2004). However, regardless of the landscape's increased ability to support black bears in recent years, social carrying capacity is ultimately an important limiting factor to bears in Vermont. Social carrying capacity, described as the density and distribution of a species that humans will tolerate (Foster et al. 2002), is largely shaped by cultural values, public awareness and management (Bettigole 2012; Haskell et al. 2010).

According to a recent report conducted for the Vermont Fish and Wildlife Department, despite the increasing level of bear-related complaints (Spencer et al. 2007), the majority of Vermont residents (57%) would like to see the black bear population remain the same in their county or slightly increase (16%) while only 7% would like to see the population decrease. Major reasons cited for a desire to see increased bear populations were improved chances of seeing black bears, ecological importance and aesthetics. The primary reason for wanting a decrease in the black bear population was to reduce human-bear conflicts (Duda et al. 2007).

The relationship between humans and black bears is complex. In one Massachusetts study, farmers that had experienced direct economic loss as a result of black bear crop depredation still perceived black bears as deserving tolerance and valued their presence on the landscape (Jonker et al. 1998). This relationship is further complicated by the lack of substantial understanding of factors that may influence consumption of human foods. Black bears are known to seek anthropogenic foods such as agricultural crops and garbage in Vermont (Hammond 2002), and reports of damage often increase in years with shortages of natural food crops (Jonker et al. 1998). However, there are several other factors that influence black bear consumption of

anthropogenic food and human-bear conflict, such as individuality (i.e. the case of a single young male repeatedly damaging bee hives, garbage receptacles, barbeques and livestock), human compliance with recommendations to contain garbage and bird seed, an expanding bear population and hunting limitations (Hammond 2002).

A population of 4,500 to 6,000 bears is considered to be a desirable goal for the Vermont black bear population to optimize public hunting opportunity, maintain biological sustainability and satisfy residents (Haskell et al. 2010). Increased policy regarding human-bear conflicts, outreach and public education and the use of hunting and bear hounds to keep bears wary of humans are methods employed by the Vermont Fish and Wildlife Department to reduce human-bear conflict (Haskell et al. 2010). Managing human-bear conflict is challenging for management agencies such as the Vermont Fish and Wildlife Department. Having a greater understanding of factors that might lead to black bear consumption of human foods will aid in future decisions regarding human-bear conflict mitigation and social carrying capacity (Merkle et al. 2011).

2.3 Stable Isotope Analysis

2.3.1 Stable isotope analysis and wildlife

Traditionally, wildlife diet studies have been based on direct observation, stomach content analysis (Crawford et al. 2008) and most commonly, scat analysis (Beeman and Pelton 1980; Eagle and Pelton 1983; Hewitt and Robbins 1996). Scat analysis describes ingested diet by examining non-digestible items and does not describe assimilated diet (Hewitt and Robbins 1996; Robbins et al. 2004). Scat analysis can result in biased estimates of diet due to differential digestibility of food items (Hewitt and Robbins 1996).

Easily digestible foods may be underrepresented (Newsome et al. 2010) and the importance of less digestible foods may be overestimated when frequency of occurrence is used to analyze scat composition (Hewitt and Robbins 1996). Fecal correction factors used to compensate for the difference between scat and actual food consumed can be difficult to estimate and apply (Hilderbrand et al. 1996). To overcome some of the inherent biases of traditional methods, naturally occurring stable isotopes have been used in recent nutritional studies to estimate assimilated diet (Robbins et al. 2004).

Stable isotope analysis provides a means to determine dietary resources that have been assimilated into animal tissue, and allows researchers to quantify and characterize the diet of a species (Ben-David and Flaherty 2012). Many elements exist in two or more forms known as isotopes, one of which is often significantly more abundant (Crawford et al. 2008). Stable isotopes of elements have differing numbers of neutrons in the nucleus, resulting in different masses (Robbins et al. 2004). Isotopes can be assimilated into an organism's tissues, and unlike radioactive isotopes, stable isotopes do not decay over time (Crawford et al. 2008). Stable isotope analysis quantifies the relative abundance of two target isotopes of a particular element. Due to differing physical properties related to atomic mass, isotopes of the same element behave differently in chemical and physical reactions resulting in natural variation in the ratio of heavy to light isotopes found in organic tissues (Ben-David and Flaherty 2012).

The process of fractionation results in changes in isotopic ratios that can be analyzed in a variety of organic compounds (Crawford et al. 2008). There are two distinct forms of fractionation, referred to as equilibrium fractionation and kinetic fractionation. Equilibrium fractionation happens when heavier isotopes create stronger

bonds than the light isotopes of the same element, with either the product or the substrate. Kinetic fractionation occurs when a single type of molecule changes phase or when the reaction occurring is non-reversible, and often occurs in enzymatic processes, diffusion and evaporation (Ben-David and Flaherty 2012). When multiple processes are involved in creating a measurable difference between original components and products, the changes are referred to as discrimination (Ben-David and Flaherty 2012).

Variations in ratios between heavy and light isotopes of an element, described in parts per thousand or per mil (‰), are measured relative to an international standard and expressed in delta notation (δ) in the following equation:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) * 1000$$

δ is the isotopic notation (called delta)

X is the element in its heavy form

R is the ratio of heavy to light isotope of the element.

For example, the ratio of ^{13}C to ^{12}C is expressed as $\delta^{13}C$ (Boutton 1991). Samples which contain more of the heavier isotope of an element than the standard are commonly known as 'enriched' samples, while those samples with less of the heavy isotope are referred to as 'depleted' samples (Crawford et al. 2008). Small variations in ratios are measured with high-precision dual-inlet gas isotope ratio mass spectrometers (Boutton

1991) or continuous flow mass spectrometers (Ben-David and Flaherty 2012). The former allows for repeated measurements of a sample prepared off-line.

Comparative amounts of target stable isotopes in animal tissues and diets vary due to natural fractionation that occurs when diet tissues are assimilated into consumer tissues. Because consumer tissues are synthesized directly from dietary components, tissues often reflect the isotopic composition of food (Crawford et al. 2008). It is important to apply fractionation factors before comparing isotopic composition of food items to isotopic composition of consumers. The proportion of isotopes within various animal tissues such as hair, blood, or bone are compared to samples of food items to quantify diet components (Koch 2007). Stable isotopes have been used to examine diet composition as an alternative and complement to traditional methods, in a variety of mammals such as mustelids, canids, felids, ursids as well as extinct animals (Ben-David et al. 1997a; Burns et al. 1998; Hénaux et al. 2011; Hilderbrand et al. 1996; Newsome et al. 2010). Stable isotope analysis offers benefits over traditional methods of diet studies such as ability to measure diet over the time frame represented in the tissue sample (e.g. time between last molt and collection for hair samples, lifetime for bone) (Greenleaf 2005), ability to examine factors that might influence unique individual diets such as sex or age group (Hilderbrand et al. 1996), and ability to quantify food habits of animals that are difficult to observe (e.g. elusive or extinct animals) (Jacoby et al. 1999). Because carbon and nitrogen are primarily taken up by consumers through diet (Ben-David and Flaherty 2012), stable isotopes of these elements (^{13}C, ^{12}C ; ^{15}N, ^{14}N) are frequently analyzed in diet studies (Ben-David and Flaherty 2012).

2.3.2 Carbon

Carbon isotopes ($\delta^{13}C$) are typically used in vertebrate diet analysis as a result of consistent and predictable trends that allow consumer values to reflect $\delta^{13}C$ values of primary producers (Koch 2007). Photosynthetic pathway is the primary control in carbon fractionation and field studies have proven that consumer tissues reflect the differences in $\delta^{13}C$ values characteristic of plants that utilize either the C_3 or C_4 pathways (DeNiro and Epstein 1978; Smith and Epstein 1971). When isotopic fractionation effects occurring during incorporation of dietary carbon are taken into account, the $\delta^{13}C$ value of animal tissue can describe the isotopic composition of the animal's diet (DeNiro and Epstein 1978). If diet sources have significantly differing $\delta^{13}C$ values, the relative contribution of potential diet components can be summarized (DeNiro and Epstein 1978). Plants that utilize the C_3 pathway are most common, occurring in ecosystems with cool growing seasons and have a mean $\delta^{13}C$ value of ca. -27‰ (-22‰ to -35‰) (Koch 2007). Plants that utilize the C_4 pathway evolved for low-CO_2 conditions in water-stressed environments and are more common in warm, equatorial regions (Koch 2007). Although both C_3 and C_4 plants preferentially fix ^{12}C-bearing CO_2 due to the weaker bonds associated with ^{12}C (Fry 2006), C_4 plants show lower preference for the lighter isotope, resulting in higher $\delta^{13}C$ values compared to C_3 plants (Ben-David and Flaherty 2012; mean ca.-13‰, -9‰ to -19‰: Koch 2007). The standard comparative value used in stable isotope analysis of $\delta^{13}C$ is Vienna Pee-Dee Belemnite (VPDB) (Coplen 1996; Slater et al. 2001).

2.3.3 Nitrogen

Nitrogen in animal protein is primarily supplied by dietary protein, and can therefore be useful in determining trophic levels at which consumers are feeding (Hobson et al. 2000; Hopkins et al. 2012; Koch 2007). The measurable increase in $\delta^{15}N$ at each trophic level (between 2‰ and 4‰, Kelly 2000) allows direct inferences to be made regarding consumer diet (Crawford et al. 2008) (but see Ben-David and Flaherty 2012). The preferential removal of ^{14}N from ingested food in the digestive track of animals in urea and uric acid causes enrichment of consumer tissues relative to food items consumed (Kelly 2000). The standard comparative value used in stable isotope analysis of $\delta^{15}N$ is atmospheric nitrogen (AIR) (Hoering and Moore 1958; Slater et al. 2001).

2.3.4 Discrimination factors

Using stable isotope analysis to examine the relative contributions of food sources to consumer diet relies on an inherent assumption that there are predictable relationships between the isotopic composition of food sources and the isotopic composition of consumer tissues (Bond and Diamond 2011). However, this assumption is invalid for several reasons: 1) isotopic fractionation occurs during assimilation of dietary isotopes to consumer tissues; 2) assimilation efficiencies of consumers vary; and 3) tissue-specific allocation of nutrients exists (Gannes et al. 1997). These factors create differences between the isotopic composition of tissue and diet, which is known as tissue to diet discrimination and denoted as ($\Delta = \delta_{tissue} - \delta_{diet}$). Discrimination is alternatively referred to as: fractionation factors, fractionation, enrichment and trophic enrichment (Cerling and Harris 1999). Discrimination is the preferred term because it refers to the fact that there

are many processes that potentially influence the differences in isotopic composition between diet and consumer tissues (Martínez del Rio et al. 2009). Fractionation is a term that references just one of many processes that create discrimination: the factors that cause differences between reactants and products in chemical reactions (Ben-David and Flaherty 2012). Trophic fractionation refers to the difference between a whole organism and its diet as a result of many physiological processes (Martínez del Rio et al. 2009). Discrimination factors have been cited as the weakest link in the use of stable isotopes and mixing models to predict proportional contributions of diet items to consumer tissues (Bond and Diamond 2011; Gannes et al. 1997), and there is need for greater understanding of the effects of diet and other factors on discrimination values (Kurle et al. 2014). The selection of appropriate discrimination values may be the most important assumption researchers make in applying stable isotopes to questions related to diet reconstruction (Florin et al. 2011).

The incorporation of isotopic signatures from diet sources into consumer tissues is complex (Ben-David and Flaherty 2012). The efficiency of assimilation of sources into consumer tissues may vary among tissues from the same species or the same individual, among the same tissues from the same species when consuming different diets, or within a given tissue in an individual (Dalerum and Angerbjörn 2005; Martínez del Rio et al. 2009; Parng et al. 2013). Animal factors that may influence discrimination by specific tissues include intake rate, nitrogen excretion method, metabolic rate, isotope routing, growth rate (Florin et al. 2011), trophic level, body condition (Gannes et al. 1997), sex, and age (Kurle et al. 2014). Isotope incorporation into tissues has also been found to be allometrically related to body mass (Carleton and del Rio 2005). Within

macromolecules, the dynamics of isotope ratios are influenced by metabolic routing where nitrogen in tissues is assimilated from dietary amino acids and carbon in tissues is assimilated from dietary protein, carbohydrates and lipids (Hobson and Quirk 2014), which subsequently influences the isotope ratios within the whole tissue (Dalerum and Angerbjörn 2005). Digestive physiology of animals can also play a role in isotope routing (Kurle et al. 2014). In addition, physiological condition can influence isotope ratios in tissues, where starving and water-stressed animals have isotopically distinct tissues from non-stressed animals (Dalerum and Angerbjörn 2005; Gannes et al. 1997). Because growing animals route more dietary protein to tissue growth than animals that are not rapidly growing, less N is removed as waste and nitrogen discrimination factors are lower (Kurle et al. 2014). Different tissue types have been shown to have differing discrimination factors within the same individual (Caut et al. 2008; Tieszen 1978), where hair, due to the amino acid composition of keratin often has higher $\Delta^{13}C$ values than other tissues (DeNiro and Epstein 1978; Kelly 2000; Kurle et al. 2014), lipids can be depleted and bone collagen can be enriched in ^{13}C relative to other tissues (Hobson and Quirk 2014).

There are several dietary factors that may contribute to differences in isotope discrimination. Dietary proteins and lipids can have different isotopic signatures and be incorporated into tissues at different rates due to metabolic routing, resulting in variation in discrimination factors among consumer tissues (Caut et al. 2008). For example, dietary protein quality and quantity are two major hypothetical causes of nitrogen discrimination differences. In some studies, as protein content of diet increases, $\Delta^{15}N$ has been shown to increase (Kelly and Martínez del Rio 2010; Martínez del Rio et al. 2009).

Kurle et al. (2014) argues that carnivores on high protein diets shed extra ingested protein through waste flux resulting in higher $\Delta^{15}N$ values as compared to herbivores on lower protein diets with lower waste flux. This may be supported by the fact that increased digestibility of animal protein as compared to plant protein may lead to greater retention of ^{15}N (Kurle et al. 2014). Alternatively, Robbins et al. (2010) predicted that consumers foraging at higher trophic levels would have decreased nitrogen discrimination factors. This has been supported in some studies, where $\Delta^{15}N$ has decreased with greater ingestion of protein (Hobson and Quirk 2014). Protein quality may also affect discrimination of nitrogen isotopes, where $\Delta^{15}N$ increases as protein quality decreases (Robbins et al. 2005; Roth and Hobson 2000). In addition to proteins, lipid content may influence tissue discrimination factors; higher-lipid content in prey may create more hair macromolecules derived from lipids, resulting in decreased ^{13}C values relative to animals ingesting lower-lipid dietary items (Parng et al. 2013). Finally, variations in dietary amino acids can affect discrimination factors for consumer uptake of both carbon and nitrogen (Parng et al. 2013). This is further complicated by the fact that even when consuming isotopically homogeneous diets, isotopic composition of consumer tissues vary depending on what dietary tissues consumer tissues are synthesized from (e.g. lipid created from dietary carbohydrate vs. dietary lipid) (Gannes et al. 1997). Differences in discrimination factors can therefore be expected between animals that gain nutrition and energy from proteins and lipids as compared to carbohydrates (Hobson and Quirk 2014).

Discrimination factors in omnivores are especially difficult to estimate due to the mixed diets that these animals consume. For instance, isotopic routing in omnivores consuming meat that is a good source of protein and plants that are sources of

carbohydrates will lead to an underestimation of the contribution of plants to diet in the isotopic composition of consumer tissues. This is because it is more energetically efficient to catabolize carbohydrates (from plants) directly while depositing lipids and assimilating protein into tissues (from meat) (Gannes et al. 1997). Seasonally consumed diets would make estimation of discrimination factors simpler, while mixed diets may add the effect of dietary protein complementation to discrimination. These discrimination factors vary with temporal changes in food consumption and complementation and are not necessarily linear, additive or constant in nature (Robbins et al. 2010). Even factors such as photosynthetic pathway of plants consumed may influence variation in $\Delta^{13}C$ among consumer tissues (Roth and Hobson 2000).

Mixing models require that accurate tissue to diet discrimination factors are applied. Unfortunately, if discrimination factors are specific to many factors related to consumer, tissue and diet, choosing incorrect discrimination factors may lead to inaccurate estimations of proportions of dietary sources (DeNiro and Epstein 1978; Martínez del Rio et al. 2009). The use of proxy discrimination factors estimated for species or even tissues other than a study's specific focal species and tissues may not be appropriate (Bond and Diamond 2011). The sensitivity of mixing models and subsequent estimates of relative proportional contributions of food sources to variability in discrimination factors is well documented (Bond and Diamond 2011; Milakovic and Parker 2013). While large differences between consumer and diet isotope ratios may diminish the error caused by discrimination factor estimation (Martínez del Rio et al. 2009), smaller differences between source and consumer isotope ratios when combined with estimated discrimination factors may produce erroneous results (Bond and Diamond

2011). Although specific effects of incorrect discrimination factor choice may vary depending on the nature of the model being utilized, discrimination factors directly influence the relative locations of food sources and consumers in the mixing space, which is an important part of the mixing model analysis (Newsome et al. 2012).

The reliance on discrimination factors that are assumed and not experimentally derived can lead to inaccurate estimations of diet reconstruction. Because species-specific discrimination factors are often not available, it is extremely common for researchers to utilize alternative discrimination factors based on similar species (Bond and Diamond 2011). There are several methods researchers have employed in selecting proxy discrimination factors, including: 1) using a mean for all foods which may not take into account variation; 2) feeding captive animals specific diets and measuring discrimination factors; 3) developing regressions between discrimination values and dietary isotopic ratios that describe general relationships or provide specific formulas (Florin et al. 2011); 4) using mean values from compiled reviews of the literature; 5) using values from similar species fed on comparable diets; 6) using values from similar species fed on very different diets (Martínez del Rio et al. 2009); and 7) using historic values from the literature (Δ^{15}N:3‰, Δ^{13}C:1‰) (Ben-David and Flaherty 2012; DeNiro and Epstein 1978).

Since recent calls for more research on diet to tissue discrimination factors (Gannes et al. 1997; Martínez del Rio et al. 2009), there have been several studies dedicated to the task of summarizing current discrimination factors used in published studies (Caut et al. 2009; Dalerum and Angerbjörn 2005), studies that provided insight into discrimination factor variability through lab experimentation (Ben-David et al.

1997b; Caut et al. 2008; Hobson and Quirk 2014; Kurle et al. 2014; Parng et al. 2013; Robbins et al. 2010), and studies that have assessed the potential effects that discrimination factor choice may have on diet reconstruction results (Bond and Diamond 2011; Milakovic and Parker 2013). There is still a need for controlled lab studies to assess the factors that may influence discrimination and provide species-specific values (Dalerum and Angerbjörn 2005), and an equally important need for studies that examine the discrimination factors for wild carnivores and omnivores (Hobson and Quirk 2014). It would also be beneficial if future studies would continue to report isotopic differences between consumer tissues collected at the same time (Milakovic and Parker 2013). Finally, any studies that estimate variability in discrimination factors for omnivores specifically are greatly needed (Caut et al. 2008), as the complexities involved in mixed diet consumption are still not well understood. In the future, discrimination factors may have to be predicted parameters that require extensive additional information, rather than the pre-determined estimates used today (Florin et al. 2011). Studies that estimate variance about discrimination factors may allow more realistic estimation of diet composition when appropriate species and tissue specific discrimination factors are not available, and reporting ranges of potential proportional contributions of food sources to diet may be a more realistic goal for researchers given the complex nature of discrimination factors (Hobson and Quirk 2014).

2.3.5 Concentration dependencies

When stable isotope analysis is used to reconstruct diet through mixing models, several important assumptions are made. One such assumption is that the proportion of

N derived by the consumer from a single source is equal to the proportion of C the consumer derives from that same source (Phillips and Koch 2002). This may be a reasonable assumption for consumers feeding on a single group of foods that have a narrow range of differences in C and N concentrations and therefore low variability in C:N ratios. However, if a consumer feeds on multiple groups of foods with a wide range of C and N concentrations, the initial assumption of equal C:N ratios among food sources is inaccurate (Hopkins and Ferguson 2012). In omnivore diets, one source is often richer or poorer in an element (i.e., meat with low C:N, plants with high C:N), resulting in a proportionate increase or decrease of the source's contribution to the mixture when compared to other sources (Phillips and Koch 2002). Therefore, concentration dependent models are recommended for use when elemental concentrations vary widely, and standard linear mixing models should only be used when elemental concentrations do not vary, or to test sensitivity of predicted proportional contributions to isotopic composition of diet sources (Koch and Phillips 2002; Phillips and Koch 2002).

Concentration dependent models take into account different C and N contributions based on elemental concentrations and isotopic values (Phillips et al. 2014). Robbins et al. (2002) questioned the usefulness of concentration dependent models for diet reconstruction of complex systems such as omnivorous bear diets as concentration dependent models require extensive pre-existing knowledge about the system and food sources as well as large assumptions. However, in some scenarios, concentration dependent models have been shown to have improved predictive power over concentration independent linear models (Woodcock and Walther 2014).

Although elemental concentrations of food sources are relatively simple to measure, it may not be appropriate to use the elemental concentrations of ingested foods when mixing models really assess the relative proportions of assimilated foods, not ingested foods. Digestibility and macromolecular composition (% carbohydrate, % lipid, % protein) must, therefore, be incorporated into concentration data to better estimate assimilated diet (Koch and Phillips 2002; Robbins et al. 2002). Digestibility corrected concentration dependent models may require more assumptions and may be impractical for some studies due to the increased amount of preliminary data needed (Robbins et al. 2002). In some scenarios, C and N concentrations of different food groups may be more similar after digestibility information is included in concentration data than the corresponding raw C and N concentrations, although this would not be known until after calculations are done (Phillips et al. 2014). While original mixing models such as IsoConc (Phillips and Koch 2002) accommodate these data for two-element three-source systems, for studies investigating diets of omnivores, it is suggested that a concentration dependent mixing model corrected for digestibility be used that can handle any number of sources, such as SIAR (Parnell et al. 2010), IsotopeR (Hopkins and Ferguson 2012), or MixSIAR (Stock and Semmens 2013) (Phillips et al. 2014).

2.3.6 Alternative factors that may influence stable isotope values

It is important to remember that carbon and nitrogen isotopic compositions in individual consumer tissues are influenced by a variety of factors other than trophic position and photosynthetic pathway of producers (Ben-David and Flaherty 2012). Body size, nutritional status, age and assimilation efficiency are just some of the factors that

may affect the rate of isotope incorporation (Martínez del Rio and Carleton 2012), while variations in discrimination between consumer tissue and diet among species and individuals (Ben-David and Flaherty 2012) may add to the problem. For example, the accumulation of ^{15}N throughout a consumer's lifetime may make age a stronger determinant of $\delta^{15}N$ than diet for some species. This was evident in a study examining walleye in Lake Champlain, Vermont (Overman and Parrish 2001).

Isotope values of primary producers are extremely variable and influenced by climate, $\delta^{15}N$ of soil, root depth, water availability, differences in nitrogen fixation rates and atmospheric carbon and nitrogen isotopic composition (Ben-David and Flaherty 2012; Kelly 2000). Soil moisture and temperature can affect evapotranspiration and efficiency of water use, thereby influencing stomatal conductance and photosynthetic rates in C_3 plants of the same species (Ben-David and Flaherty 2012). In addition to this, not all parts of a plant are always equivalent in terms of isotopic values, due to biosynthetic pathways (Marshall et al. 2008).

Geographical differences can have dramatic effects on isotopic values, with soil $\delta^{15}N$ directly influencing plant $\delta^{15}N$ values (Marshall et al. 2008). For example, terrestrial plants vary extensively in $\delta^{15}N$ values with foliage values ranging from between -8‰ and 3‰ in some areas (Peterson and Fry 1987) and ranging up to 18‰ in desert plants (Kelly 2000). This disparity may be explained by rainfall abundance, where the potential for nitrogen loss from a system is greater in areas with lower rainfall and increased rainfall reduces the openness of the nitrogen cycle (Austin and Sala 1999). In a South African study, C_3 plants in arid ecosystems exhibited high $\delta^{15}N$ values relative to

C_3 plants found in wetter ecosystems, perhaps reflecting greater nutrient availability in arid ecosystems (Swap et al. 2004).

Plant type, other than photosynthetic pathway, can also influence isotopic value. For example, the $\delta^{15}N$ values of nitrogen-fixing plants are often low relative to non-nitrogen fixing plants, and the $\delta^{15}N$ values of deep rooting plants are often high relative to shallow rooting plants (Kelly 2000; Koch 2007; Virginia et al. 1989). The potential impact of these influences extends to the consumer level. In one example, lemurs (*Lepilemur leucopus*) in Madagascar foraging on nitrogen-fixing legumes had low $\delta^{15}N$ values relative to lemurs that foraged less often on legumes (Schoeninger et al. 1998). In a second example, a study of San Joaquin kit foxes (*Vulpes macrotis mutica*) in California indicated that individuals in urban areas had significantly lower $\delta^{15}N$ values than foxes in rural areas (Newsome et al. 2010). This may have been a result of the lower $\delta^{15}N$ values found in human foods grown in the U.S. with synthetic fertilizers (Nardoto et al. 2006). This trend was also documented in a study examining feral cats as introduced predators, where $\delta^{15}N$ of muscle tissue was lower than expected based on stomach content analysis, perhaps a result of feeding on garbage or processed pet food that contained foods grown with synthetic fertilizers (Meckstroth et al. 2007).

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values of primary producers can also vary based on marine vs. terrestrial environment, and freshwater vs. marine systems. Primary producer $\delta^{13}C$ values appear to increase from offshore to near shore areas and mean $\delta^{13}C$ values may be higher in marine systems than in freshwater systems (Koch 2007). In coastal regions, $\delta^{15}N$ may be greater due to deposition of marine material (Heaton 1987). In a study of herring gull eggs, $\delta^{15}N$ was found to decrease as the proportion of aquatic

foods consumed by parents decreased relative to the proportion of terrestrial foods consumed by parents. However, $\delta^{13}C$ values of gull eggs from adult gulls feeding on terrestrial foods were high relative to gulls feeding on aquatic foods, perhaps evidence of terrestrial foods containing corn, or other C_4 plants (Hebert et al. 1999).

Finally, it is important to account for decreases in atmospheric carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic values due to human-use of fossil fuels in long-term studies (Ben-David and Flaherty 2012). These additional factors that influence carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values in producers and consumers, while complex, also create new potential applications that broaden the range of opportunities for use of stable isotope analysis. Studies should be designed to minimize the effects of factors other than those which they are targeting for use in specific analyses.

2.3.7 Bayesian stable isotope mixing models for diet analysis

Stable isotope mixing models (referred to as mixing models) are commonly used by ecologists to determine the proportional contribution of assimilated food sources to consumer diet. Early frequentist mixing models such as IsoError (Phillips and Gregg 2001) can be applied to systems where the number of sources does not exceed $n + 1$ (n = number of isotopes analyzed) without being underdetermined and can incorporate various sources of error. However, this model produces nonsensical results when any consumer data points fall outside of the mixing space (the bounding polygon formed when lines are used to connect sources in a multivariate mixing space) and does not incorporate flexibility with regards to assumptions (Hopkins and Ferguson 2012). In IsoConc, Phillips and Koch (2002) improved upon the mixing model framework by incorporating

'concentration dependence' to challenge the common assumption that elemental concentrations of dietary items are equal: an assumption that may be invalid especially in cases of omnivores foraging at various trophic levels on food items that differ in C:N ratios. Following suggestions made by Robbins et al. (2002), the digestibility of macronutrients in food sources was incorporated into a revised model (Koch and Phillips 2002). Although the model improved upon the ability of mixing models to accurately determine dietary source contributions, it did not include a way to incorporate the sources of error inherent to mixing models (Hopkins and Ferguson 2012). A third frequentist mixing model, IsoSource, allowed the number of sources to exceed $n + 1$ (Phillips and Gregg 2003). This model works by using a standard linear mixing model and systematically calculates each combination of possible source contributions by a given increment (summing to 1.0). The model then predicts isotope values for each possible combination using mean source isotope values and determines whether the values are feasible given a designated mass balance tolerance which incorporates measurement error and source variability (Hopkins and Ferguson 2012). Phillips and Gregg (2003) suggested that the entire range of feasible solutions be reported rather than any one combination.

Bayesian stable isotope mixing models fit probability models that incorporate various sources of uncertainty, numbers of sources exceeding $n + 1$, prior information (a probability distribution representing prior knowledge) and hierarchical frameworks to isotopic data (Hopkins and Ferguson 2012). MixSIR, an early model, estimates proportional contribution to diet by importance sampling and incorporates discrimination factors, individual or population-level consumer data, and a Dirichlet prior on

proportional estimators (Moore and Semmens 2008). A second iteration of this model is hierarchical and can estimate diets at either the individual or population level by using information from the population-level to estimate individual diets (Semmens et al. 2009). However, when population sample sizes are large, individual estimates may be skewed towards the mean; the ideal sample size for estimating individual diets is unknown (Hopkins and Ferguson 2012). Another Bayesian mixing model, SIAR, allows for the incorporation of concentration data and uses R as an interface (Inger et al. 2008; Jackson et al. 2009; Parnell et al. 2010). IsotopeR (Hopkins and Ferguson 2012), MixSIAR (Stock and Semmens 2013), and FRUITS (Fernandes et al. 2014) are recently published models that allow flexible model specification in a Bayesian statistical framework, which incorporate many features (e.g., uncertainties, concentration dependence, any number of sources, covariates, hierarchical structure) (Phillips et al. 2014).

Bayesian statistics allows for intuitive interpretation of results and can incorporate prior information and uncertainty by using probabilities to assign degrees of belief to parameter values or hypotheses (McCarthy 2007). This approach is useful for ecologists seeking to gain an improved understanding of the truth, given uncertainty. Criticisms of Bayesian methods include difficulties in defining priors and the inherent subjectivity of interpretations (McCarthy 2007). Bayesian models calculate posterior probabilities ($Pr(\theta|x) \approx \pi(\theta) \times L(x|\theta)$), given prior information ($\pi(\theta)$) and the likelihood of data given the parameter ($L(x|\theta)$). Priors can be informative, based on pre-existing knowledge of the system (e.g. knowledge about dietary proportions based on an alternative diet analysis method) (Derbridge et al. 2012), or uninformative and allow

inferences to be unaffected by pre-existing information (also known as flat, diffuse, or uninformative) (Hopkins and Ferguson 2012).

MixSIAR integrates many advances recently made in Bayesian mixing model theory (Stock and Semmens 2013). MixSIAR builds on the original Bayesian mixing model framework proposed in MixSIR (Moore and Semmens 2008) and incorporates: 1) residual error terms suggested in SIAR (Inger et al. 2006); 2) up to two categorical covariates incorporated as either fixed or random effects (Semmens et al. 2009); 3) concentration dependence and uncertainty in discrimination and source values (Parnell et al. 2010); 4) up to one continuous covariate (Francis et al. 2011); and 5) isometric log ratio (ilr) transformation (Parnell et al. 2013). Stock and Semmens (2013) intend to include multivariate residual error (Parnell et al. 2013) and the ability to specify priors other than uninformative priors in future versions.

In MixSIAR, uninformed priors are assigned to source means, precisions and global population proportion means are drawn from an uninformative Dirichlet distribution and the global population distribution is transformed using the isometric log ratio (ilr) approach (Stock and Semmens 2013). MixSIAR uses Markov Chain Monte Carlo (MCMC) methods to simulate draws that are slightly dependent and approximately from a posterior distribution using the JAGS algorithm (Just Another Gibbs Sampler) (Gelfand and Smith 1990; Plummer 2003; Stock and Semmens 2013). Program users may specify number of chains, burn-in length and thinning of sample draws. Longer chain lengths allow for convergence on the true posterior distributions and thinning may reduce the dependence between sample draws. In this way, MixSIAR estimates the

entire distribution of proportional contributions of each potential food source to consumer diet (Stock and Semmens 2013).

2.3.8 Stable isotopes and bears

Stable isotope analysis has been used in diet studies on many bear species such as American black bear (*Ursus americanus*) (Hobson et al. 2000; Hopkins et al. 2012; Merkle et al. 2011), Asiatic black bear (*U. thibetanus*) (Mizukami et al. 2005), brown bear (*U. arctos*) (Hobson et al. 2000; Jones et al. 2006; Mowat and Heard 2006), polar bear (*U. maritimus*) (Horton et al. 2009) and extinct cave bear (*U. spelaeus*) (Hilderbrand et al. 1996). As with other wildlife studies, bear diet studies utilizing fecal analysis may suffer from inherent biases, such as a range of digestive efficiency from 30% for vegetative matter and >90% for animal matter (Hewitt and Robbins 1996; Pritchard and Robbins 1990). Therefore, studies using scat analysis may underestimate the role of animal matter or anthropogenic food in bear diets. This is especially true regarding anthropogenic food sources that may not contain identifiable indigestible material, unlike most natural foods (Newsome et al. 2010).

There are many examples of how stable isotope analysis has been used to gain a better understanding of bear diets around the world. A study in Missoula, Montana found that there was no difference in diet between urban and wildland bears (Merkle et al. 2011). These data suggest that garbage is not an important diet component of urban bears in Missoula and conflict may be related to a few individual animals and may not be reflective of the population. In Yosemite National Park, California, stable isotope analysis was used to identify food conditioned bears and examine proportional

contribution of different foods to diets of food-conditioned bears (Hopkins et al. 2012). Results indicated that reactive human-bear management did not change the status of known food-conditioned bears and did not reduce the amount of human food in the diets of food conditioned bears. Ben-David et al. (2004) examined blood and hair samples from females and males to determine whether male and female diets significantly differed between seasons and found that some female brown bears with young may be altering foraging behavior to avoid the risk of infanticide on crowded stream corridors. Hilderbrand et al. (1996) estimated the diets of brown bears and extinct cave bears using stable isotope analysis of several bear tissues and found that there was little fractionation across bear tissues with the exception of adipose tissue. Hobson et al. (2000) examined carbon and nitrogen stable isotopes of black bears and brown bears in British Columbia and found that there was significant overlap in the diets of the two species except for female grizzly bears, which had lower $\delta^{15}N$ values. This study confirmed that both bears are primarily herbivorous and cubs dependent on milk were found to be at a trophic level higher than adult females. Jacoby et al. (1999) used stable isotopes to examine the current and historical diets of brown and black bears in several areas in the western United States and Alaska and found that bear diet varies greatly between specific populations. Mizukami et al. (2005) estimated nuisance bear dependence on human food sources in Japan. Findings showed that rural bears had elevated carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values relative to alpine bears, although carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) levels fluctuated greatly over the length of the hair for rural bears, suggesting opportunistic feeding habits. Mowat and Heard (2006) found that meat was more important for some populations of grizzly bears than others.

Carbon and nitrogen isotopes have been used to examine the relative contribution of human foods to black bear diet (Hopkins et al. 2012; Merkle et al. 2011; Teunissen Van Manen 2011). The natural diet of the American black bear in temperate zones consists almost exclusively of plants that utilize the C_3 photosynthetic pathway (Hilderbrand et al. 1996). Potential prey species also preferentially forage on C_3 plants and have isotopic signatures that represent consumed vegetation (DeNiro and Epstein 1978; Jacoby et al. 1999). Although some anthropogenic food resources utilized by black bears, such as apples or berries from orchards or farms (Greenleaf et al. 2009; Merkle et al. 2013), may not have distinguishable isotopic signatures from native C_3 foods (Hilderbrand et al. 1996; Merkle et al. 2011), most human foods and packaging contain ingredients derived from corn (*Zea mays*). Corn is a plant with a C_4 photosynthetic pathway and therefore has a distinct isotopic signature from more common C_3 plants (Smith and Epstein 1971). Bears may have ^{13}C-enriched tissues as a result of eating human garbage (e.g. corn by-products, meat produced from animals raised on corn diets or corn-based packaging) or directly feeding on corn in agricultural fields (Hopkins et al. 2012; Koch 2007). Bears that pose a management problem or occur nearby to human development have been found to have elevated levels of $\delta^{13}C$ relative to other bears (Hobson et al. 2000; Mizukami et al. 2005). Due to natural increase in $\delta^{15}N$ with trophic level increase in natural food webs, bears with elevated $\delta^{15}N$ values may be consuming natural animal tissues or meat-rich human garbage (Hopkins et al. 2012). $\delta^{15}N$ values in bear hair may be useful for predicting whether bears in primarily herbivorous populations are feeding on garbage (Greenleaf 2005; Greenleaf et al. 2009).

CHAPTER 3: JOURNAL ARTICLE

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Running head: Stable isotopes and bear diet in Vermont

Using stable isotope analysis to estimate black bear (*Ursus americanus*) diet in Vermont

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3.1 Abstract

The black bear (*Ursus americanus*) is an iconic species with cultural, economic and ecological importance in Vermont, USA. Bears exhibit a highly variable diet, and few studies have described bear diet in the state. Information on diet may provide insight into foraging behavior, thus allowing managers to better assess patterns of human-bear conflict. My objectives were to estimate the relative contribution of food items to bear diet and how factors including sex, habitat, food availability, and nuisance status describe patterns of consumption. I collected samples from bears and major food groups including C_3 plants, white-tailed deer (*Odocoileus virginianus*), corn (*Zea mays*), and human foods, then quantified diet using stable isotope analysis. Samples were collected from 71 bears, 547 plants, and 38 deer throughout Vermont. I also collected 12 corn samples, and 20 human hair samples to represent anthropogenic foods. I determined $\delta^{13}C$ and $\delta^{15}N$

isotope values for all samples, then used Bayesian mixing models to estimate the contribution of foods and effect of each factor on proportional contribution estimates. Nuisance status best described patterns of diet over other factors. Median percent contributions for non-nuisance bears were 73.2% C_3 plants, 23.8% corn, 1.9% human foods, and 0.5% deer. Median percent contributions for nuisance bears were 64.6% C_3 plants, 28.9% corn, 3.2% human foods, and 0.7% deer. Factors such as sex, habitat, and food availability exerted less effect on diet than expected. Proportional contribution of meat was lower than in some other parts of North America, suggesting bears forage differently in Vermont. Results provide the first statewide estimate of bear diet and indicate corn may represent a much larger component of diet than previously thought. In particular, bears labeled as nuisance animals may forage on greater proportions of corn throughout the year.

3.2 Key Words

Ursus americanus, anthropogenic subsidies, stable isotope ecology, diet, human-wildlife conflict, bear

3.3 Introduction

The black bear (*Ursus americanus*) is an iconic species that embodies cultural, economic and ecological importance in Vermont, USA. Recent growth in the bear population combined with an increasing level of land development and fragmentation have resulted in a higher occurrence of bears within developed areas and increased reports of human-bear conflict (Haskell et al. 2010). Black bears demonstrate substantial

tolerance for human presence and are often perceived as a nuisance species due in part to their consumption of anthropogenic foods such as garbage, bird seed and agricultural crops (Foster et al. 2002). Black bears have an omnivorous diet (Larivière 2001), and are characterized as opportunistic foragers (Bastille-Rousseau et al. 2011). However, relatively little is known about the proportional contribution of food items to black bear diet in Vermont. Black bears in Vermont are managed through habitat conservation, a legal hunting season, and nuisance bear control (Haskell et al. 2010). A greater understanding of diet is needed to provide insight into foraging behavior and allow managers to better assess patterns of anthropogenic food consumption.

Black bear diet components have been identified in a scat analysis study conducted at Stratton Mountain, Vermont (Hammond 2002) and a stomach content analysis study conducted on bears harvested in northeastern Vermont (Willey 1978). Both studies found that black bears mainly consume vegetation. In the Stratton Mountain study, Jewelweed (*Impatiens capensis*), Jack-in-the-pulpit (*Arisaema triphyllum*), and tall nodding sedge (*Carex gynandra*) were most frequently consumed, whereas meat only made up a small portion of black bear diet (Hammond 2002). Although the hair and hooves of white-tailed deer (*Odocoileus virginianus*) fawns were found in early summer bear droppings (Hammond 2002), there is evidence that bears in northern forests only opportunistically feed on fawns when foraging for preferred vegetation (Bastille-Rousseau et al. 2011). Stomach analysis of bears in northeastern Vermont revealed that apples (*Malus* spp.) were consistently the most frequently consumed fall food item, whereas jewelweed, chokecherry (*Prunus virginiana*), American beech (*Fagus grandifolia*) nuts, oak (*Quercus* spp.) acorns, grasses and carrion varied in importance

throughout the fall (Willey 1978). In addition to natural food sources, the Stratton Mountain study identified several sources of anthropogenic food. Cereal crops such as corn (*Zea mays*) are high quality food sources that are readily utilized by bears, especially at the interface of croplands and natural habitat (Mattson 1990). Corn can be an important component of black bear diet in the northeast, and black bears may travel large distances to access cornfields (Hammond 2002). Garbage, another anthropogenic food source, is often cited as being a major attractant to black bears (Badyaev 1998; Spencer et al. 2007) due to its high caloric content and predictable availability (Beckmann and Berger 2003a) and black bears in Vermont have been observed raiding garbage cans and birdfeeders (Hammond 2002). Both the Stratton Mountain scat analysis study and the northeastern Vermont stomach analysis study analyzed bear samples from limited areas within the state, and results may not be representative of the statewide population.

Several factors may influence black bear foraging patterns, such as the distribution and availability of food resources (Amstrup and Beecham 1976). For example, American beech nuts are an important mast crop used by black bears in the northeastern United States, and the abundance of this crop influences foraging strategy as well as reproductive schedules (McLaughlin et al. 1994). Scarcity of natural foods has been found to result in black bears foraging in agricultural areas (Elowe and Dodge 1989; McDonald and Fuller 2001; McLaughlin et al. 1994) and cause an increase in the frequency of human-bear conflict reports (Mattson 1990). Alternatively, the availability of anthropogenic foods may be more important to bears foraging on non-natural foods than the availability of natural foods (Merkle et al. 2013). There may also be a difference between male and female foraging behavior. In the western United States, larger,

heavier, and more dominant males occupy the most food rich habitats, including urban areas (Beckmann and Berger 2003b). Adult male black bears are generally larger than females (Willey 1978), occupy larger home ranges than females (Amstrup and Beecham 1976; Hammond 2002), and may have increased opportunity to forage on human foods.

Traditional methods of estimating diet such as scat analysis and stomach content analysis, although widely used, have inherent drawbacks and biases. For example, stomach content analysis is an invasive procedure and samples from harvested animals only provide an estimate of recently ingested food (Polito et al. 2011). Scat analysis may lead to inaccurate depictions of diet as more digestible food items may be difficult to detect and less digestible foods may be overestimated (Hewitt and Robbins 1996). Stable isotope analysis is a popular technique that provides an overall representation of diet and overcomes several of the shortcomings of traditional methods, allowing researchers to effectively characterize a consumer's diet, including contributions of anthropogenic foods (Phillips 2012).

Stable isotopes are non-radioactive forms of certain elements that differ from each other in number of neutrons in the nucleus (Fry 2006). The natural variation in the ratio of heavy to light isotopes found in organic tissues as a result of physical and chemical reactions is called fractionation (Ben-David and Flaherty 2012). Variations in ratios of heavy to light isotopes of an element, described in parts per thousand (‰; per mil), are measured relative to an international standard using a mass spectrometer (Fry 2006). Because consumer tissues are synthesized directly from dietary components, tissues often predictably reflect the isotopic composition of food if the discrimination between consumer and source tissues is accounted for (Crawford et al. 2008). The

relative proportions of isotopes within various consumer tissues (e.g. hair, blood, bone) are compared to the isotopic values of diet items to quantify diet composition (Koch 2007).

Differences in the ratio of heavy (^{13}C) to light (^{12}C) carbon isotopes ($\delta^{13}C$) in consumer tissues reflect variation in $\delta^{13}C$ values of diet items. For example, plants that utilize a C_3 photosynthetic pathway have tissues with more negative $\delta^{13}C$ values than C_4 plants, which are enriched in the heavy carbon isotope (^{13}C) (Smith and Epstein 1971). Nitrogen isotope ratios ($\delta^{15}N$) of consumer tissues can be useful, in some systems, for determining the trophic levels at which consumers are feeding (Hobson et al. 2000) due to the preferential removal of ^{14}N from ingested food and subsequent enrichment of consumer tissues relative to food items consumed (Kelly 2000). Photosynthetic pathway of primary producers and trophic level are only two of a multitude of factors that affect isotopic signatures in food sources and consumers (Ben-David and Flaherty 2012).

Stable isotope analysis of carbon and nitrogen has been used to describe the diet of American black bears (Fortin et al. 2013; Hobson et al. 2000; Hopkins et al. 2014a; Jacoby et al. 1999; Merkle et al. 2011; Teunissen van Manen et al. 2014), Asiatic black bears (*Ursus thibetanus*) (Mizukami et al. 2005), brown bears (*U. arctos*) (Ben-David et al. 2004; Bentzen et al. 2014; Edwards et al. 2011; Felicetti et al. 2003; Hopkins et al. 2014b; Jones et al. 2006; Mowat and Heard 2006), polar bears (*U. maritimus*) (Horton et al. 2009), and extinct cave bears (*U. spelaeus*) (Bocherens et al. 2014; Hilderbrand et al. 1996; Robu et al. 2013). In temperate zones, the natural diet of American black bears consists mostly of plants that utilize the C_3 photosynthetic pathway (Hilderbrand et al. 1996) and animals that preferentially forage on C_3 plants (Jacoby et al. 1999). Although

some anthropogenic food resources utilized by black bears, such as fruit crops (Greenleaf et al. 2009; Merkle et al. 2013), may not be isotopically distinguishable from native C_3 food sources (Merkle et al. 2011), any anthropogenic foods consisting of corn, a C_4 plant (Smith and Epstein 1971), may be isotopically distinct from native foods. As a result, bears may have ^{13}C-enriched tissues as a result of eating human foods in garbage (e.g. corn by-products, meat produced from animals raised on corn diets, corn packaging) or as a result of feeding on corn grown for human consumption and silage (Hopkins et al. 2012; Mizukami et al. 2005). High $\delta^{15}N$ values in bear tissues may be the result of feeding on natural animal tissues or meat-rich human garbage, and in primarily herbivorous populations may indicate human food consumption (Greenleaf et al. 2009; Hopkins et al. 2012).

This study used stable isotope analysis of carbon and nitrogen to quantify and better understand the diet of black bears in Vermont. The objectives were to assess the relative contributions of major food items to diet and examine the influence of four factors on diet composition, including: sex, habitat, food availability, and nuisance status.

3.4 Materials and Methods

3.4.1 Study area

The study occurred throughout the state of Vermont in the northeastern United States. Mean elevation in Vermont is 370 m ranging from a low of 30 m at the edge of Lake Champlain in the east to 1,339 m on the peak of Mount Mansfield in the Green Mountains of the central part of the state (Long et al. 2007). Climate is humid continental with mean statewide temperatures ranging from -10°C to -5.5°C in January

and from 17.7°C to 21.0°C in July (Thompson and Sorenson 2000). Annual precipitation ranges from 75 cm in the Champlain Valley to more than 180 cm in the southern peaks of the Green Mountain ridge (Thompson and Sorenson 2000). Vermont is over 70% forested and characterized by many upland and wetland natural communities (Thompson and Sorenson 2000). Although natural open areas do exist to some degree, most open areas are a result of human development and agricultural usage (Thompson and Sorenson 2000).

3.4.2 Sample collection

Black bear hair samples

I used hair samples from individual bears to estimate diet. Black bear hair samples were collected between 1999 and 2004 by the Vermont Fish and Wildlife Department from bear carcasses throughout the state with the exception of Grand Isle County, where bears do not occur. Causes of mortality for bears included non-nuisance mortality (i.e. harvest by hunters, road mortality, starvation; n = 63) and nuisance euthanasia (n = 8). Hair samples were placed in sealed plastic bags, labeled with harvest date, sex, town of harvest and mortality type and stored until analysis.

Black bears have two types of hair: underfur and guard hair. Underfur grows in late summer and fall (C. T. Robbins, pers. comm. in Teunissen van Manen et al. 2014 and Jones et al. 2006). Guard hair grows at a constant rate beginning at different times in the spring and early summer, depending on nutrition (Felicetti et al. 2004; Jones et al. 2006; Van Daele et al. 2013), and grows until hibernation (Ben-David et al. 2004; Mizukami et al. 2005). Black bears molt once a year in late spring to early summer but may delay

molt to late summer or early fall if nutrition is severely limited (Jacoby et al. 1999). Because underfur and guard hair represent different growth periods, they may represent different diets. Guard hair and underfur may have significantly different isotopic signatures within individual bears (Jones et al. 2006). I selected long, whole guard hairs when possible, including underfur only when sufficient quantities of whole guard hairs were unavailable.

Food source samples

I collected samples of major food items to assess their relative contributions to bear diet. Food sample groups included C_3 plants, deer, human foods, and corn. I opportunistically collected C_3 plant samples and deer hair samples in all counties with bears. I collected samples of the nine most common natural C_3 plant items found in the Stratton Mountain black bear study (Hammond 2002) under the assumption that these items represent the most important components of bear diet in the state. Plant species collected include American beech (*Fagus grandifolia*) nuts and leaves, blackberry (*Rubus* spp.), cherry (*Prunus* spp.), Jack-in-the-pulpit (*Arisaema triphyllum*), jewelweed (*Impatiens capensis*), oak (*Quercus* spp.), raspberry (*Rubus* spp.), tall nodding sedge (*Carex gynandra*), and wild apple (*Malus* spp.). In summer of 2013, I collected a maximum of five subsamples of each plant species on private property with landowner permission and at Wildlife Management Areas. I collected hair from deer carcasses during the fall 2013 hunting season. Adult deer hair samples were assumed to represent opportunistically consumed fawns or carrion.

I opportunistically collected corn samples from Vermont gardens, croplands, and seed growers. I pooled Vermont corn samples with samples grown in other parts of the country; samples grown outside of Vermont had indistinguishable isotopic values when compared to local samples. Human hair samples were collected to estimate the isotopic values of human foods (e.g. garbage, compost). I collected samples from discarded floor clippings at two hair salons in Burlington, Vermont in 2013. I assumed that human hair signatures were consistent across the state because human food is obtained most often from grocery stores that source food from the same distributors.

3.4.3 Sample preparation

I sonicated hair samples in glass beakers containing deionized H_2O for two 3-minute intervals using a tabletop ultrasonic cleaner to remove coarse debris. I then rinsed samples under a ventilation hood in 2:1 chloroform-methanol solution to remove oils and fine debris (Merkle et al. 2011). After allowing the samples to dry in aluminum weighing boats under the ventilation hood for 15 minutes, I transferred hairs to an oven to dry overnight at 50°C. Hair samples were then stored in clean plastic sample bags.

I combined the subsamples of each C_3 plant species into a single bulked sample per species per county. All samples, including corn, were dried in an oven for several days at 50°C. When completely dry, I milled the samples into a fine homogeneous powder with a ball mill and stored them in 20 ml plastic sample vials.

3.4.4 Sample analysis

Stable carbon isotopes

Whole hair and milled plant samples (ranging in weight from 1 to 10 mg) were loaded into pre-combusted quartz tubes (6 mm OD) along with cupric oxide (600 mg) and reduced granular copper (500 mg) (Boutton 1991). I attached the sample tubes to a tube-sealing manifold connected to a vacuum pump, and sealed the tubes using a gas/oxygen torch after a vacuum of $<10^{-2}$ torr had been reached. I combusted the samples by heating the sealed tubes in a furnace at 900^{o}C for two hours, and then allowed them to cool overnight. CO_2 was separated from the other two products of the combustion, H_2O and N_2, using cryogenic distillation. Finally the isolated CO_2 from the samples was analyzed on a VG SIRA Series II (VG, United Kingdom) dual-inlet mass spectrometer to obtain the $\delta^{13}C$ values.

Stable nitrogen isotopes

I loaded whole hair and milled plant samples (ranging in size from 5.0 to 15.0 mg for hair samples; 45.0 to 100.0 mg for plant samples) into pre-combusted (one hour at 900°C) quartz tubes (9 mm OD) along with cupric oxide (2.5 g) and granular copper (2.0 g) (Kendall and Grim 1990). I filled pre-combusted quartz tubes (6 mm OD) with calcium oxide and heated these tubes in a furnace at 1000°C for one hour. I placed the 6-mm OD tubes inside the 9-mm OD tubes containing the sample and reagents and sealed the 9-mm OD tubes on a vacuum manifold after removing all air from the samples. The sealed sample tubes were combusted for two to four hours at 850°C followed by slow cooling overnight. After attaching the combusted sample tubes to the dual-inlet mass

spectrometer, I cracked them using a tube-cracker to release the N_2 gas and obtain $\delta^{15}N$ values.

Data summarization

I reported carbon and nitrogen isotope results as per mil (‰) using the delta notation (δ):

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) * 1000$$

where δ is the isotopic notation, X is the heavy form of the element (^{13}C or ^{15}N), and R_{sample} and $R_{standard}$ are the ratios of heavy to light isotope (e.g. $^{13}C/^{12}C$) of the sample and standard, respectively. The standard for C is Vienna PeeDee Belemnite (VPDB). The standard for N is atmospheric air (AIR). Measurement precision is ±0.1‰ for $\delta^{15}N$ and ±0.5‰ for $\delta^{13}C$ based on replicate reference materials and internal-lab standards.

Elemental analysis (%C, %N and C/N)

A subset of plant samples from two counties was analyzed for percent organic carbon (%C) and percent nitrogen (%N). I weighed powdered samples (3 to 6 mg) in tin capsules and analyzed them using a CE Instruments NC 2500 Elemental Analyzer (EA) (CE Instruments, United Kingdom). The EA was calibrated using known standards: low organic sediment standard OAS B-2152 (1.65±0.02% C, 0.14 ±0.01% N) and high organic sediment standard OAS B-2150 (6.72 ±0.17% C, 0.50 ±0.01% N). To ensure

accuracy of the measured values, sets of standards were run as unknowns before, during and after each sample run. Based on replicate analysis, sample precision was within 1% of the quantity measured. C/N ratios, by mass, were calculated using the %C and %N results.

3.4.5 Mixing model analysis

I used a mixing model approach in a Bayesian framework to estimate probability distributions for the contribution of potential food items to bear diet (Hopkins and Ferguson 2012). This framework allows multiple sources of uncertainty (e.g. discrimination values) to be incorporated into estimates (Moore and Semmens 2008). An assumption of the Bayesian stable isotope mixing model approach is that all food sources are included, as models can only estimate the relative contributions to diet of foods analyzed (Phillips 2012). Although Bayesian mixing models allow a larger number of sources than traditional mixing models, which are underdetermined when using more than $n + 1$ food sources (n = number of isotopes analyzed), Bayesian mixing models are better able to estimate diet composition when fewer sources are included (Phillips et al. 2014). I aggregated C_3 plant species into a single food source to contrast between logically defined food sources that may constitute black bear diet (Phillips et al. 2005), such as natural plant species (C_3), anthropogenic plant species (C_4), natural animal tissue (deer), and human foods. Preliminary ANOVA tests confirmed that both $\delta^{13}C$ and $\delta^{15}N$ values of different plant species were significantly different overall (p-values of 2.2×10^{-16} and 1.1×10^{-6}, respectively) (Figure A-5.1), while $\delta^{13}C$ and $\delta^{15}N$ values of plants collected in different counties were not significantly different (p-value > 0.05) (Figure A-5.2).

Mixing models require that sources be isotopically distinct (Ben-David et al. 1997b) and are able to more precisely estimate diet proportions with more distinct sources (Phillips 2012). I used non-parametric Mann-Whitney *U* tests to determine whether food groups were isotopically distinct for $\geq$ 1 isotope at the 0.05 significance level (Derbridge et al. 2012) and found that all four bear food sources were isotopically distinct for $\geq$1 isotope value (Table A-5.1).

I analyzed stable isotope data in a series of models using the MixSIAR GUI v2.1 model framework which uses the open source languages R and JAGS (Just Another Gibbs Sampler) (Parnell et al. 2013; Plummer 2003; R Core Team 2014; Stock and Semmens 2013). Models in MixSIAR GUI v2.1 are fit using a Markov Chain Monte Carlo (MCMC) method to estimate the probability density functions of variables using uninformative priors. This method estimates the entire posterior distribution for each variable by simulating potential proportion estimates from which Bayesian credible intervals and summary statistics can be calculated. Gibbs sampling was conducted on each model using 3 chains in JAGS with a chain length of 1,000,000, a burn-in of 700,000 and thinning rate of 300. Discrimination factors and concentration dependencies were integrated into the models.

To estimate the proportional contribution of food items to diet, I created both a base model incorporating process error (MixSIR model method; Moore and Semmens 2008) and individuals as residual error and a base model incorporating both process error and residual error (SIAR model method; Parnell et al. 2010). I ran independent base models to examine the effect of using elemental concentration dependency data vs. concentration dependencies that incorporate digestibility, and reported base model results

to facilitate comparison among mixing model estimates of different black bear populations.

I examined the relative effects of covariates (i.e. sex, nuisance status, hard mast productivity rating, and habitat land cover) on dietary proportion estimates. I developed a model set that included all individual covariates and additive combinations of covariate pairs. Categorical covariates were incorporated as fixed effects and individuals were incorporated as random effects in the model. I ran an additional model that did not incorporate individuals as random effects when posterior plots indicated that the variation in diet between individuals was less than the variation in diet as a result of a categorical random effect. When incorporating individuals as random effects, I included process error but no residual error; I included residual error only when individuals were not analyzed as random effects. Continuous covariates were analyzed by incorporating individuals as random effects and including process error. Trace plots and the Gelman-Rubin diagnostic were used to assess convergence (Gelman et al. 2003). Deviance Information Criterion (DIC) values were calculated for each model (Semmens et al. 2009; Spiegelhalter et al. 2002). The level of support for models was determined by DIC value relative to the model with the lowest DIC using guidelines developed for ranking AIC (McCarthy 2007): 0-2 ΔDIC indicated substantial support, 4-7 ΔDIC indicated considerably less support and >10 ΔDIC indicated essentially no support (Burnham and Andersen 2002). Results for the best ranked model were summarized as mean, standard deviation, median and 95% Bayesian credible intervals for proportional contributions of each food source.

3.4.6 Discrimination factors

Differences between isotope ratios of consumer tissues and diet sources are known as tissue to diet discrimination factors and denoted as ($\Delta = \delta_{tissue} - \delta_{diet}$). Discrimination is the result of fractionation during metabolic transformations and stoichiometric effects such as isotopic routing (Martínez del Rio et al. 2009). Discrimination may vary among tissues in an individual, among the same tissues from same-species individuals feeding on different diets, or within a single tissue in an individual (Dalerum and Angerbjörn 2005; Martínez del Rio et al. 2009; Parng et al. 2013). Many components may influence variation in discrimination factors, including: sex, age (Kurle et al. 2014), trophic level, body condition, nutritional status (Gannes et al. 1997), changes in isotope ratios as a result of individual physical or chemical reactions (fractionation), dietary intake rate of isotopes, nitrogen excretion method, metabolic rate, isotope routing, and growth rate (Florin et al. 2011). Dietary factors such as protein quality and quantity (Kelly and Martínez del Rio 2010), lipid content, amino acid variations (Parng et al. 2013) and what dietary tissues are synthesized into consumer tissues may also influence discrimination (Gannes et al. 1997).

Due to their complex nature, researchers are often unable to estimate discrimination factors unique to each food source and system. Therefore, discrimination factors are typically extracted from published research (Ben-David and Flaherty 2012). Discrimination factors from the literature are assumed to be true and applicable to the data they are applied to. However, choosing values developed for other studies or averaging discrimination factors from data that should not be pooled can potentially lead to errors in mixing model calculations and incorrect results (Caut et al. 2009; DeNiro and

Epstein 1978). Additionally, discrimination factors based on captive studies may be inappropriate for use in studies examining the diets of free-ranging animals (Kurle et al. 2014).

I estimated discrimination factors for diet sources by averaging values used in recent isotope studies of bear diet elsewhere (Table A-5.2). I applied $\delta^{13}C$ discrimination factors of 3.1‰ and 3.0‰ and $\delta^{15}N$ discrimination factors of 3.9‰ and 4.3‰ to meat and plant food source values, respectively. Discrimination factors were added to food source isotope values when creating the isotopic mixing space.

3.4.7 Concentration dependency

An assumption commonly made when using stable isotope analysis to reconstruct consumer diet with mixing models is that the proportion of C derived by the consumer from a single source is equal to the proportion of N the consumer derives from that same source (Phillips and Koch 2002). Because omnivores, such as bears, may feed on multiple groups of food with a wide range of C and N concentrations, it would be incorrect to assume that C:N ratios of all contributing food sources are equal (Hopkins and Ferguson 2012). A bear's diet might consist of a mixture of meats with low C:N ratios and plants with high C:N ratios, which would result in proportionately increased or decreased estimated contributions of each food source to the mixture (Phillips and Koch 2002). Because mixing models estimate proportional contributions to diet based on assimilated food sources, not ingested food sources, digestibility and macromolecular composition (% carbohydrate, % lipid, % protein) may be necessary components of concentration calculations (Koch and Phillips 2002; Robbins et al. 2002).

Dietary elemental concentrations and concentrations incorporating digestibility were measured, calculated and borrowed from previous studies for each food source. I used concentration values for average weighted human diet that incorporate digestibility (Digest [C]; Digest [N]) which were reported by Hopkins and Ferguson (2012); I calculated elemental concentrations for average weighted human diet from data Hopkins and Ferguson (2012) collected from the USDA National Nutrient Database (NDB) (U.S. Department of Agriculture: Agricultural Research Service 2014), using equations derived from Robbins (1993) as cited in Phillips and Koch (2002). I calculated deer and corn Digest [C] and Digest [N] as well as elemental concentrations ([C],[N]) using data from the NDB and equations from Hopkins and Ferguson (2012) and Koch and Phillips (2002). I measured [C] and [N] for two samples of each C_3 plant species on an elemental analyzer using samples collected in Vermont in summer of 2013. Digest [N] and Digest [C] for C_3 plants were calculated using these elemental concentrations and calculations from Hopkins and Ferguson (2012) and Koch and Phillips (2002), with the exception of beech nuts and acorns. Beech nut and acorn Digest [C] and Digest [N] were calculated using equations from Hopkins and Ferguson (2012), Koch and Phillips (2002) and digestibility information from a pine nut study (Mealey 1980). Robbins (1993) provided much of the nutrition information that informed calculations (protein is 52 wt% C, 16 wt% N; lipid is 75 wt% C, 0 wt% N; carbohydrate (including fiber) is 45 wt% C, 0 wt% N). Robbins et al. (2002) calculated dry matter digestibility (Digest DM) averages for leafy plants and fruits based on published data (McLellan and Hovey 1995; Pritchard and Robbins 1990; Rode and Robbins 2000; Rode et al. 2001; Welch et al. 1997). Making the assumption that corms are more similar to tubers than fruits or leafy vegetation, I used

tuber Digest DM calculated by Pritchard and Robbins (1990) for the Digest DM of Jack-in-the-pulpit. Carbon concentration of plant dry matter was assumed to be 45% (Barbour et al. 1987; Hopkins and Ferguson 2012; Robbins et al. 2002). I assumed that protein from meat was 100% digestible, protein from plants 90% digestible, and lipids and carbs 100% digestible for all food groups (Hopkins and Ferguson 2012).

Concentration dependence sensitivity analysis

I conducted a sensitivity analysis to evaluate the sensitivity of posterior proportional contributions of food sources to assumptions made about elemental concentrations incorporating digestibility. Koch and Phillips (2002) tested the effects of uncertainties surrounding leafy plant concentration values on dietary estimates. While assumptions about the high digestibility of plant protein (e.g. fruit) and animal protein are well validated (Robbins 1993), Digest DM for leafy plants has not been as well studied and is likely extremely variable among types of plants and consumers (Koch and Phillips 2002). Digest [C] of assimilated plant matter is often assumed to be 45% (Barbour et al. 1987), but if the only digestible portion of leafy plants is protein, digested [C] may resemble the stoichiometry of protein (52%). Likewise, when consuming lipid-rich foods (e.g. seeds), digested [C] might be similar to the stoichiometry of lipids (75%) (Koch and Phillips 2002). I examined the sensitivity of diet estimates by varying Digest [C] between 45-60%, and varying Digest DM between 15-55%, a range of values similar to those determined to be realistic by Koch and Phillips (2002). To test the effects of digestibility assumptions in a scenario in which the plant food source consists of both plant protein and plant leafy matter, sensitivity analyses were conducted at three levels:

1) Digest DM and Digest [C] were varied only for leafy plant matter, assuming digestibility estimates for plant protein were reliable; 2) Digest DM was varied only for leafy plant matter assuming Digest DM was estimated accurately for plant protein, but Digest [C] was varied for all plant matter; 3) Digest DM and Digest [C] were varied for all plant matter.

3.4.8 Factors affecting diet

Mast

In Vermont, the primary hard mast crop used by black bears is American beech (Faison and Houston 2004) and in some parts of the state, oak (*Quercus* spp.) (Hammond 2002). I used Hard Mast Production Rating (HMPR) data collected by the Vermont Fish and Wildlife Department (Hammond 2010) to examine the effects of natural food availability on black bear diet. The HMPR is a rating (i.e. poor, fair, good, excellent) based on average number of nuts/plot counted at 17 sites surveyed annually in Vermont (Hammond 2010). Because bear hair samples were collected over a range of time periods, hair samples collected in the same year could potentially represent diets from different years. Hair collected during the spring and early summer may represent diet from the previous year (Hopkins and Ferguson 2012). Hair collected in the late summer or fall may represent diet from the current season (Felicetti et al. 2003). Molt timing varies depending on nutrition, condition, and does not begin until bears leave dens.

Methodologies from several studies examining bear diet with stable isotope analysis of hair were reviewed (Table 3.1) and I selected August as a frequently used cut-off date for determining in which year a hair was grown. August may be a reasonable

cut-off date because some bears begin eating the current hard mast crop of beech nuts and acorns in August, especially if soft mast is not in good condition. In addition, bears in Vermont may feed on the previous year's beech nuts until late spring and the previous year's acorns until mid-July if available (F. Hammond, pers. comm.). I assumed that long guard hairs and all underfur collected prior to August were representative of the previous year's diet, whereas guard hairs and underfur collected in August and later were representative of diet in the year in which the bear was killed; hair samples likely underrepresent spring diets (Ben-David et al. 2004). Diet years were used to determine HMPR for both American beech and oak for all bear samples.

The availability of natural foods such as hard mast influence black bear movements and foraging strategies (McLaughlin et al. 1994), and scarcity of natural foods may result in bears foraging on alternative anthropogenic food sources near to areas developed by humans, such as agricultural areas (Baruch-Mordo et al. 2014; Elowe and Dodge 1989; Mattson 1990). Black bears in Vermont travel long distances to forage on corn in years of poor mast crops (Hammond 2002), and therefore, I expected that in years of poor and fair HMPR, proportional contribution of anthropogenic foods in black bear diet would be higher compared to years of good or excellent HMPR.

Habitat

I estimated the percent cover of three land cover types around the location of each bear sample (Table 3.2). Most samples were only identified to town level and not by a specific location, so I estimated land cover within the geographic boundaries of each town, buffered by the average home range diameter (10.2 km) for bears in Vermont

(Hammond 2002), to reduce bias for sample locations that may have occurred near a town boundary. Using the National Land Cover Database (NLCD), I estimated the percent cover of forest, agriculture, and developed land (Homer et al. 2007; Jin et al. 2013). All calculations were estimated using Geographic Information Systems (ArcGIS v.10.2.2, ESRI, Redlands, California, USA) and percentages were transformed into Z-scores.

Black bear site occupancy in Vermont has been found to be positively associated with percent forest (Long et al. 2011), and most life requisites can be found within various forest habitats (Mitchell et al. 2002). Therefore, I expected that black bears using areas with more forested habitat would have more access to natural foods, and less anthropogenic food in their diet. Alternatively, the availability of anthropogenic foods may be more important to bears foraging on mixed diets of natural and non-natural foods than the availability of natural foods (Merkle et al. 2013). Black bears are known to feed on corn crops where this anthropogenic food source is available (Garshelis et al. 1999; Hammond 2002), and bears located near to human development have been found to have increased levels of ^{13}C relative to other bears, indicating a diet comprised of some proportion of anthropogenic foods containing corn (e.g. garbage, corn crops) (Hobson et al. 2000; Mizukami et al. 2005). I therefore expected that bears found in areas with more land cover classified as developed, agricultural or cultivated would have a higher contribution of anthropogenic foods in diet.

Sex

Male black bears have larger home ranges than females (Hammond 2002) and have been shown to be more dominant than females and occupy preferred, food-rich habitat, including urban environments (Beckmann and Berger 2003b). In the Stratton Mountain study, male black bears were regularly observed feeding on corn in agricultural fields while females were not (Hammond 2002). I therefore expected male black bears to have more access to anthropogenic foods and posterior proportional contributions of anthropogenic foods to be higher for male bears than for females.

Nuisance Status

Consumption of anthropogenic foods represents the most common cause for human-bear conflict (Beckmann and Berger 2003a). Although many bears undoubtedly utilize anthropogenic food sources such as agricultural crops when available (Landers et al. 1979), only some bears are labeled as nuisance animals. Because little is known about the period of time for which a bear has been exhibiting nuisance behavior, it is unclear whether the diet of nuisance bears differs from that of non-nuisance bears. I expected nuisance bears to have diets with a higher contribution of anthropogenic foods than non-nuisance bears.

3.5 Results

3.5.1 Sample collection

I used 71 bear hair samples in the analysis (Figure 3.1). I collected 547 plant samples and combined samples of the same species from each county into bulk samples

(n=121). I also collected 38 white-tailed deer hair samples, 9 Vermont-grown corn samples, 3 commercially grown corn samples, and 20 human hair samples.

3.5.2 Consumer and diet source values

Isotope values of black bear hair samples ranged from -28.1 to -15.9‰ for $\delta^{13}C$ and 2.2 to 6.2‰ for $\delta^{15}N$ (Table A-5.3). The mean $\delta^{13}C$ value for bear samples was -22.5 (2.3‰; 1 SD) and the mean $\delta^{15}N$ value was 4.0 (1.0‰) (Figure 3.2). Mean isotope values for potential food sources ranged from -31.8 to -11.6‰ for $\delta^{13}C$ and -0.8 to 8.5‰ for $\delta^{15}N$ (Table 3.3). Corn had higher $\delta^{13}C$ values, ranging from -12.3 to -10.9‰, with variable $\delta^{15}N$ values (1.5 to 14.3‰). C_3 plants had a wider and lower range of $\delta^{13}C$ values than corn (-38.4 to -26.8‰), and $\delta^{15}N$ values ranged from -6.8‰ to 6.0‰. Deer hair ranged from -27.5 to -18.0‰ for $\delta^{13}C$ and 1.6 to 7.4‰ for $\delta^{15}N$. Human hair samples had the least variable range of $\delta^{13}C$ and $\delta^{15}N$ values (-18.5 to -16.5‰ and 7.7 to 9.1‰, respectively).

3.5.3 Concentration dependency

Elemental concentration of carbon [C] calculated for C_3 plant species ranged from 41.5% to 50.4% and elemental concentration of nitrogen [N] ranged from 1.9% to 2.8%. Concentration dependence values incorporating digestibility for C_3 plant species ranged from a Digest [C] of 45.0% to 57.9% and a Digest [N] of 0.5% to 7.1% (for calculations, see Table A-5.4). Because animal tissue is assumed to be 100% digestible, elemental concentrations and concentrations incorporating digestibility were the same for deer with a nitrogen concentration of 13.9% and a carbon concentration of 53.1%. [C] of corn,

beech nuts and oak acorns calculated using data from the NDB were similar to the assumed plant [C] of 45.0% but slightly higher by 1.5%, 3.0% and 0.2% respectively. Digest [C] was higher than [C] for beech nuts and oak acorns (by 9.9% and 7.1%, respectively), but slightly lower for corn by 0.7% (Table A-5.5). Human food Digest [C] and Digest [N] values were taken directly from calculations made by Hopkins and Ferguson (2012), and I estimated elemental concentrations using their raw data to equal 7.1% [N] and 53.5% [C] (Table A-5.5).

Trends were similar between the three sensitivity analyses conducted, but dietary estimates were most sensitive to assumptions made to the entire group of C_3 plants, and less sensitive to assumptions made about a small segment of the C_3 plant aggregate (leafy plants). When only leafy plants were altered through a range of plausible Digest [C] and Digest DM values, dietary estimates shifted a maximum of 2.1% across the range of Digest [C] values explored (Figure A-5.3). In contrast, when all C_3 plants were included in changes made to Digest [C], dietary estimates varied up to 6.5% between Digest [C] levels (Figure A-5.4). Corn appeared to be the most sensitive to Digest [C] assumptions, having a higher proportional contribution to diet when Digest [C] was higher and representing a wider range of proportion estimates between Digest [C] levels when Digest DM was lowest. Human food decreased in contribution with increased Digest [C] and had the largest difference in contribution between Digest [C] levels when Digest DM was highest. Human food estimates varied at most by 2.9% between levels of Digest [C], in the models where all C_3 plants were included, and deer estimates varied the least. Dietary estimates were most sensitive to changes in assumptions about Digest [C] and Digest DM when alterations were made to both parameters for all C_3 plants (Figure A-

5.5). All food source estimates were most sensitive to Digest DM assumptions at lowest [C] values and lower extremes of Digest DM values tested. Between Digest DM levels, human food estimates had the largest difference at 15.9%, decreasing in proportion at higher levels of Digest DM. Between lowest Digest DM and highest Digest DM, C_3 plant estimates increased a maximum of 8.8%, corn estimates increased a maximum of 8.7%, and deer estimates decreased a maximum of 1.5%.

3.5.4 Mixing models

Isotope values for bears fell within the range of the discrimination-corrected food source isotopic values in the mixing space (Figure 3.3), a necessary condition for mixing models (Phillips et al. 2014). For the base model (no covariates), the median posterior percent contribution was 71.9 (68.6 to 75.1%; representing 95% Bayesian credible intervals) for C_3 plants, 25.8 (21.2 to 29.4%) for corn, 1.4 (0.1 to 6.0%) for human food, and 0.4 (0.0 to 2.2%) for deer (Figure A-5.6). To test sensitivity of diet estimates to type of error incorporated and type of concentration dependence values applied, I ran three additional base models (Models 2:4; Table 3.4). In all four base models, C_3 was the most common diet item followed by corn, human food and deer. Proportional contribution estimates for food sources were similar across base models, with median percent contributions differing by a maximum of 1.8% for C_3 plant estimates, 0.7% for corn estimates, 0.2% for deer estimates, and 0.8% for human food estimates (Table A-5.6).

I examined a total of 45 models. All models that ranked better in terms of DIC value than the null model (Model 1) shared the common trait of including status as a covariate. The model that included status alone with residual error and individuals not

included as random effects (Model 17) had the most support, as the model with the lowest DIC value (Table 3.4). I compared models based on differences in DIC values relative to the lowest DIC value and found support for Models 22, 31 and 33, as they were within 10 units of the lowest DIC value (McCarthy 2007) (Table A-5.7). All other models had little support, with DIC values 50 or more units greater than the smallest DIC value. Model 22, had substantial support, while Model 31 and 33 had considerably less support (ΔDIC 4-7 more than lowest DIC value) (Table 3.4). However, the simpler Model 17 may be favored here (Spiegelhalter et al. 2002), as the higher DIC values of Model 22, 31 and 33 suggest that the additional parameters of oak HMPR, sex and beech HMPR are not justified and do not explain more of the variability than Model 17 with status only explains (McCarthy 2007).

The model with the most support (Model 17) indicates a difference between foraging habits of bears that were killed for nuisance behavior and bears that had no known nuisance status. The median posterior percent contribution for nuisance bears was 64.6 (55.8 to 73.2%; representing 95% Bayesian credible intervals) for C_3 plants, 28.9 (13.7 to 37.3%) for corn, 3.2 (0.1 to 25.1%) for human food, and 0.7 (0.0 to 8.2%) for deer (Figure 3.4). For non-nuisance bears, the median posterior proportional contribution was 73.2 (69.3 to 77.1%) for C_3 plants, 23.8 (18.9 to 28.0%) for corn, 1.9 (0.1 to 7.4%) for human food, and 0.5 (0.0 to 2.4%) for deer (Figure 3.5). Mean, standard deviation and other quantiles can be found in Table A-5.7. A joint uncertainty plot reveals that there is a strong negative correlation between both C_3 plants and human foods, and corn and human foods (Figure A-5.7).

3.6 Discussion

The management of black bears and human-bear conflict is difficult for wildlife agencies. A greater understanding of black bear food resource use has the potential to aid in decision making that seeks to reduce conflict and increase the social carrying capacity for black bears. Using stable isotope analysis and a Bayesian mixing model approach, I estimated black bear diet in Vermont and found that bears in Vermont mainly consume C_3 plants and corn and that meat and human food contribute relatively little to diet. A sensitivity analysis indicated that the model was robust to assumptions of food source digestibility. Results provide the first statewide estimate of bear diet and indicate that corn may be a more important food source than anticipated. Nuisance status best described patterns of diet over other factors such as sex, habitat, and natural food availability.

Mean isotope values for black bears in Vermont were similar to mean black bear $\delta^{13}C$ and $\delta^{15}N$ values from other regions such as Alaska (-22.5 [0.9‰; 1 SD] $\delta^{13}C$, 4.9 [1.7‰] $\delta^{15}N$; Jacoby et al. 1999) and Montana (-22.6 [1.1‰] $\delta^{13}C$, 4.7 [1.0‰] $\delta^{15}N$; Merkle et al. 2011). In Great Smoky Mountains National Park, bear isotope values were slightly lower (-25.0 [0.9‰] $\delta^{13}C$, -0.6 [0.9‰] $\delta^{15}N$; Teunissen van Manen et al. 2014). The similarity among populations may indicate that black bears forage on similar diets throughout their range. Alternatively, isotope values may be similar as a result of omnivorous feeding habits. Black bear populations may consume different combinations of food sources that lead to similar isotope values in assimilated consumer tissues as a result of the source isotope values and source combinations consumed.

The uncorrected $\delta^{13}C$ and $\delta^{15}N$ values of food sources were varied, and source groups were significantly different and occupied distinct spaces in the mixing space: a requirement for mixing models. The range of C_3 plant $\delta^{13}C$ values was larger than suggested by Marshall et al. (2008) (-35 to -25‰). Mean $\delta^{13}C$ values for C_3 plants collected in Vermont were low relative to $\delta^{13}C$ values of plants in Yellowstone National Park (YNP) (-27.5 [2.3‰]; Hopkins and Ferguson 2012), the western Rocky Mountains (-26.6 [2.0‰]; Mowat and Heard 2006), and British Columbia (-26.9 [±0.1‰; SE]; Milakovic and Parker 2013). One explanation for why the mean $\delta^{13}C$ value for C_3 plants collected in Vermont was relatively low is that two species in particular had very low $\delta^{13}C$ values. Jack-in-the-pulpit and jewelweed had very low $\delta^{13}C$ values relative to other plant species analyzed, which may be a result of physiological differences between species or tissues sampled (Figure A-5.1).

Mean $\delta^{15}N$ values for C_3 plants in Vermont were similar to C_3 plant values reported for plants in YNP (-0.8 [1.2‰]; Hopkins and Ferguson 2012), but slightly higher than values of plants in the western Rocky Mountains (-2.8 [3.0‰]; Mowat and Heard 2006) and British Columbia (-1.9 [±0.2‰; SE]; Milakovic and Parker 2013). Seger et al. (2013) reported a weighted $\delta^{15}N$ mean of -1.1 (1.9‰) for terrestrial plants and 7.5 (1.4‰) for wet-soil plants in Maine (enriched in the heavier isotope even relative to herbivores), demonstrating the extreme variability of $\delta^{15}N$ values possible in plants and subsequent difficulty in making estimations about trophic feeding level based on $\delta^{15}N$ in some systems.

Mean isotope values for human hair samples collected in Vermont closely resembled those reported in St. Louis, Missouri (-16.9 [0.8‰] $\delta^{13}C$ and 8.8 [0.5‰] $\delta^{15}N$)

which were determined to be statistically indistinguishable from a nation-wide survey of human hair (Hopkins and Ferguson 2012). The similarity between hair samples collected in Vermont and elsewhere in the United States suggests that human diet is comparable in terms of isotopic composition of foods consumed. It is likely, therefore, that human hair samples throughout Vermont would not be different isotopically from those collected in Chittenden County.

The range of $\delta^{13}C$ values for corn was smaller than has been reported for C_4 plants (-15 to -11‰; Marshall et al. 2008). However, mean $\delta^{13}C$ values for corn samples used in this study were similar to values for C_4 plants used in other studies (-11.7 [0.1‰]; Darr and Hewitt 2008). Mean $\delta^{15}N$ values for corn samples were higher than expected based on mean C_4 plant values reported in other studies (2.6 [0.2‰]; Darr and Hewitt 2008). In addition, $\delta^{15}N$ values measured for corn in this study had a much wider range than reported elsewhere (3.4 to 5.7‰; Jahren and Kraft 2008). The wide range of $\delta^{15}N$ values in my corn samples is probably explained by the fact that corn does not fix nitrogen, and therefore, $\delta^{15}N$ values of corn are dependent on the $\delta^{15}N$ of soil (Bender 1971). Soil $\delta^{15}N$ values are heavily influenced by animal manures and other fertilizers that are applied to soils (Szpak et al. 2012b). Plants grown in fields with fertilizers applied are enriched in ^{15}N relative to plants grown in unfertilized fields (Szpak et al. 2012b), and $\delta^{15}N$ values have been found to range between -0.3 and 44.7‰, depending on what plant tissue is measured, what type and how much fertilizer, if any, is applied (Szpak et al. 2012a), and what type of irrigation system is utilized (Berta et al. 2011).

Isotope values from deer harvested in Vermont closely resembled values from white-tailed deer in Alaska (-25.1 [0.8‰] $\delta^{13}C$ and 3.6 [0.8‰] $\delta^{15}N$; Derbridge et al.

2012). In addition, mean deer isotope values were similar to multi-species meat source estimates established in Montana from white-tailed deer and elk (*Cervus canadensis*) (-25.2 [1.0‰] $\delta^{13}C$ and 3.1 [1.1‰] $\delta^{15}N$; Merkle et al. 2011), and meat source estimates from a variety of animal species in YNP (-24.2 [0.7‰] $\delta^{13}C$ and 3.2 [1.0‰] $\delta^{15}N$; Hopkins and Ferguson 2012).

The results of a Bayesian stable isotope mixing model suggest that overall diet for black bears in Vermont consists mostly of natural C_3 plant food sources, and more C_4 plants (corn) than expected. Estimates of proportional contribution of food sources indicated that Vermont black bears are primarily herbivorous and consume little meat. This supports results from a study conducted in southern Vermont which reported that the primary food items identified in scat were vegetative (Hammond 2002), which is to be expected because low digestibility of plant protein is compensated for by a large intake of vegetation in populations that are primarily herbivorous (Grenfell and Brody 1983).

Black bear diet can vary substantially between populations and seasons, depending on regional and seasonal food availability (Baldwin and Bender 2009). Studies using traditional scat analysis have found black bear diets consist of a range of percent animal matter and vegetative matter: 94.9% vegetative and 2.6% animal matter in southern Yukon (MacHutchon 1989); 81% vegetative, 11% animal, and 6% artificial food in Great Smoky Mountains National Park (Beeman and Pelton 1980); and 51% vegetative and 49% animal matter in Rocky Mountain National Park (Baldwin and Bender 2009). Studies utilizing stable isotope analyses have reported a range of posterior percent contributions to diet, indicating that some populations are more herbivorous than others: diet estimates for wildland bears in Montana had a median of 39.0 (32.0 to 48.0%;

95% credible intervals) C_3 plants, 8.0 (5.0 to 12.0%) C_4 corn-based forage, and 53.0 (43.0 to 62.0%) animal matter (Merkle et al. 2011); black bear diets in Yosemite National Park consisted of a median of 72.5 (64.5 to 80.5%) plants, 10.6 (0.7 to 19.4%) animal matter, and 32.8 (17.7 to 42.5%) human food. While anthropogenic foods were found to not be a major diet source in some populations (Merkle et al. 2011), other studies report larger proportional contributions to diet (Hopkins and Ferguson 2012). Likewise, meat may contribute less to diet in some areas than others, especially where populations may have less access to large quantities of fish or ungulates (Koch and Phillips 2002). Meat has been identified as an important food source for some black bear populations (e.g. Greater Yellowstone Ecosystem, and part of the Kenai Peninsula, Alaska population), while in other populations, meat is only consumed opportunistically and vegetation is the most important food resource (e.g. Glacier National Park, Smoky Mountains) (Beeman and Pelton 1980; Jacoby et al. 1999).

My results indicate that while human foods such as garbage are probably not a meaningful food source for the Vermont bear population, corn, another anthropogenic food source, may be an important source of food. Corn was originally cultivated in the northeastern United States sometime in the eleventh century A.D. (Vogel and Merwe 1977), and there are records from early European settlers of bears damaging corn crops (Cardoza 1976). Development of quick maturing corn varieties further increased the range of corn crops, and bear populations increased as a result of more restrictive hunting regulations, leading to an increase in nuisance complaints reporting bears damaging corn in the 1980s (Garshelis et al. 1999). As a consistently available concentrated source of energy with high nutritional quality (Mattson 1990), it is not surprising that given the

opportunity, black bears would take advantage of corn crops. In some places, where corn may be heavily used in both the summer and fall (Jones and Pelton 2003), this food source is expected to substantially contribute to the nutritional welfare of bears and reduce their need to travel into residential areas in search of food (Landers et al. 1979). Bears have been found to travel long distances to reach corn and although corn is not equally available throughout Vermont (Hammond 2002), my results suggest that many bears may find opportunity to forage on corn wherever it is available.

When using stable isotope analysis and mixing models to estimate diet of consumers foraging on a variety of food sources that may differ greatly in terms of elemental concentrations, it may be necessary to incorporate these different concentrations into calculations of posterior proportional contributions of food sources (Phillips and Koch 2002). In addition, because digestibility of food sources vary, it is important to incorporate digestibility in concentration values for food sources (Robbins et al. 2002). Results from base model analyses and a sensitivity analysis suggested that this particular model and contributing data set are robust to assumptions of concentration dependence. The largest changes in estimates of dietary contributions were a result of assumptions of dry matter digestibility (Digest DM), where lower values of Digest DM caused different diet estimates than higher values of Digest DM. This difference was most apparent when Digest DM was altered for all contributing plant samples, protein and herbaceous. However, because Digest DM for plant protein has been experimentally evaluated to a greater extent than for leafy plants (Koch and Phillips 2002), it is unlikely that in many scenarios Digest DM would be assumed to be as low as 15% for all contributing plant samples. The food source most sensitive to assumptions of Digest DM

was human food, reflecting the sensitivity of human food estimates to dietary [N]. At lower digestibility levels, protein may dominate digested dry matter resulting in a rise in Digest [N] and a decrease in C:N ratio. This in turn would result in an increase in the proportion of human food in diet and a decrease in estimated corn and C_3 plants in diet. Although the dietary estimates were relatively insensitive to assumptions made about digestibility, and did not exhibit extreme differences between assumptions of Digest DM or Digest [C], this may not be the case in all scenarios. The ability of concentration-dependent models to provide accurate results depends on a greater understanding of food stoichiometry and digestibility of food sources (Koch and Phillips 2002).

I hypothesized that factors such as sex, nuisance status, oak and beech mast condition and habitat would influence food selection by black bears in Vermont and that differences in feeding patterns would be measurable using a stable isotope mixing model. The model with the most support, and models with substantial support all identified nuisance status as an important factor in diet estimates. Because it may be inappropriate to select a single best model (Spiegelhalter et al. 2002), I reported posterior proportional contributions of food items from four top models (Table A-5.7). However, the best model explaining the maximum level of detail in the simplest way possible (McCarthy 2007), may be Model 17, the model incorporating status alone as a covariate, as the similar but higher DIC score of the more complex model incorporating status and oak hard mast production rating (HMPR) indicated no new information is gained.

Nuisance status of bears in this study indicated bears that were killed as a result of nuisance behavior. Non-nuisance bears did not indicate that bears were not food-conditioned or did not engage in nuisance behavior, only that they died as a result of

other causes and had no established nuisance status. Median proportional contribution results indicate that bears with nuisance status may forage on slightly more corn and human food than the general population. These results may confirm beliefs that behavior resulting in nuisance status designation and often, lethal management, is indicative of a diet pattern which regularly incorporates anthropogenic foods. Although this is assumed to be true, without an average measure of diet, it is difficult to know for how long bears have been exhibiting nuisance behavior involving anthropogenic foods and whether it is a one-time event or a long term diet pattern. Hopkins et al. (2012) found that $\delta^{15}N$ values of bear hair were useful in confirming the nuisance status of bears in Yosemite, while $\delta^{13}C$ was not, which reinforced similar conclusions made by Hobson et al. (2000). These results provide some support for suggestions made by Beeman and Pelton (1980) and Merkle et al. (2011) that a few individual bears may be responsible for a majority of foraging on anthropogenic food sources, whereas the overall population exhibits a foraging pattern incorporating less anthropogenic foods. However, posterior distributions of corn and human foods for nuisance bears overlapped posterior distributions for non-nuisance bears, indicating that not all possible combinations of sources for nuisance bears demonstrated higher corn and human-food consumption than non-nuisance bears. Teunissen van Manen et al. (2014) found that nuisance status had no support as an indicator of anthropogenic food use, and Mizukami et al. (2005) determined that at least one bear killed for purported nuisance behavior and anthropogenic foraging was not dependent on corn, implying that nuisance behavior may not always indicate a different pattern of feeding behavior and that lethal management of bears may not always identify the correct individuals. Future studies may benefit from an analysis of hair segments to

reveal anthropogenic foraging patterns between seasons and identify bears that forage on anthropogenic foods during short time periods, as whole hair analysis may dilute evidence of anthropogenic foraging (Hopkins et al. 2012). I did not predict whether or not non-nuisance bears were food-conditioned and consumed anthropogenic foods as other studies have done (Hopkins et al. 2012; Mizukami et al. 2005), but identifying additional nuisance bears within the population would help strengthen the analysis.

I found little support for the hypothesis that males would have higher contributions of anthropogenic foods in diets than female bears. Male bears have been found to have larger home ranges, disperse farther, have greater overlap of home ranges with human development (Baruch-Mordo et al. 2014; McLean and Pelton 1990) and were more prevalent among a population of food-conditioned bears (McLean and Pelton 1990). However, my results are supported by evidence that in some wild populations, there may be no correlation of isotope values with sex (Hobson et al. 2000; Teunissen van Manen et al. 2014).

My results also indicate little support for models incorporating measures of natural food availability, in particular, oak and beech hard mast production ratings (HMPR). I hypothesized that black bear diets would have higher contributions of anthropogenic foods in years in which mast production was low. Some support was found in the second best model for oak HMPR as an indicator of foraging patterns, specifically, in years of excellent oak HMPR diet composition may consist of more C_3 plants and less anthropogenic foods than in years of poor oak HMPR. Availability of beech nuts have been found to influence weight gain, time of denning, survivorship of adult bears and mortality of cubs (Hammond 2002) and bad mast years for both beech

and acorn have shown strong associations with increased $\delta^{15}N$ values (Seger et al. 2013; Teunissen van Manen et al. 2014). It is expected that opportunistic omnivores such as bears would seek out high quality human foods especially in years of poor natural food crops (Grenfell and Brody 1983), and bears have been found to travel extensively to research anthropogenic food sources and have greater overlap with human development during these years (Baruch-Mordo et al. 2014). Hard mast abundance may explain variation in annual human-bear conflict levels (LaMere 2012; Ryan et al. 2007) and the number of nuisance bears is correlated with beech nut productivity in some regions (Oka et al. 2004). Other natural foods, including soft mast available earlier in the season have been found to share periodicity with beech nut productivity cycles, suggesting that hard mast may be a good indicator of overall natural food availability (LaMere 2012; Oka et al. 2004).

There are several explanations for why more support was not found for hard mast influence on diet patterns. First, my results could be accurate and hard mast production may not greatly influence feeding habits of Vermont bears. Because acorns and beech nuts have high nutritional value, bears may seek out this food supply wherever it is available (Grenfell and Brody 1983) and variable production levels at different sample sites indicate that even in years in which overall HMPR is poor, individual sites may have higher levels of mast production (Hammond 2010). Bears are known to travel long distances to seek food resources, and despite low abundance of oak in some parts of Vermont (Hammond 2002), bears may be able to locate acorns and beech nuts to forage on. Alternatively, there may be adequate alternative natural foods to support bears even in years of hard mast crop failure. Teunissen van Manen et al. (2014) found that only a

low number of bears transitioned from non-nuisance to nuisance status in years when hard mast crops failed, suggesting bears had enough alternative food sources other than anthropogenic foods, and Merkle et al. (2013) found that natural food availability did not describe when bears foraged near houses. Hammond (2002) found that tall nodding sedge, jewelweed and Jack-in-the-pulpit were the primary foods during spring and early summer. Jewelweed was also used throughout the summer and fall and was more abundant in diets in years of poor mast quality. Jack-in-the-pulpit is an important summer food, with the corm rivaling acorns and beech nuts in nutritional value. It may be that the consistent availability of these three plant species throughout Vermont may be substantial enough to limit the need for bears to forage on anthropogenic foods during poor hard mast years. Second, there is the possibility that my results are not accurate. HMPR may not be a reliable measure of the availability of hard mast to black bears in Vermont due to variability in production between stands in a given year, low number of total plots sampled consistently, and inability to sample across the state due to limited time and resources. Alternatively, segmenting hairs may have allowed me to focus on the period of intense feeding, or hyperphagia which coincides with the period of hard mast availability (Baruch-Mordo et al. 2014). Other studies of black bear diet have found that segmenting hairs reveals seasonal differences in foraging patterns (Darimont et al. 2007; Mizukami et al. 2005).

There was little support for models including habitat parameters as covariates. I hypothesized that black bears in areas with a greater percentage of forested land would have more access to natural foods and therefore have less anthropogenic food contribution to diet than bears in areas with less forest habitat. Black bear site occupancy

has been documented to be positively associated with percent forest, and bears are dependent on forest habitat for many of their life requisites (Long et al. 2011). I also hypothesized that black bears in areas with greater percentages of agricultural or developed land would have greater ability to access anthropogenic sources of food, and therefore, anthropogenic food would have a greater contribution to diet. Merkle et al. (2013) found that the probability of a bear foraging in developed areas was driven more by the availability of anthropogenic foods than the availability of wildland foods and although that same study found that garbage was not the main attractant, Beckmann and Lackey (2008) found that necropsied bears in urban areas had stomachs full of garbage. Bears that pose management problems or are found nearby to human development have been found to have elevated $\delta^{13}C$ levels relative to other bears (Hobson et al. 2000; Mizukami et al. 2005).

My results may be accurate, and there might be no relationship between the percent of forest, agricultural or developed land and diet patterns. Because of the ability of bears to travel extensively to seek out food resources, bears may be able to access both anthropogenic and natural food items regardless of how little is available. It is also possible that my results are not accurate, and alternative methods may have better captured the influence of habitat parameters on diet patterns. First, because the finest scale of location data available to me was at the town level, the buffered areas I examined were necessarily large and may have encompassed too much area to be useful in estimating which habitat parameters influenced black bear foraging. Even if exact kill site had been available, it would be difficult to know exactly which areas a bear was utilizing based on a single point. To better estimate habitat parameters for home ranges

utilized by bears, tracking may be necessary (Baruch-Mordo et al. 2014; Hammond 2002).

This study required that a number of important assumptions be made. First, all food sources are assumed to be included in the mixing space. Bears, as omnivores, may feed on any number of sources, and it would be impractical to attempt to collect samples from all potential food sources. The categories of C_3, deer, human food and corn are meant to approximate the four major sources bears may feed on given the assumption that other potential meat sources would be similar to deer, other C_4 plants would be similar to corn, and other C_3 plants would be indistinguishable from those which I sampled. Unfortunately, the similarity between natural C_3 plants and anthropogenic food sources that consist of C_3 plants mean that this mixing model is unable to distinguish between natural plant foods and fruit orchards, non-corn compost, and any C_3 agricultural crops (Merkle et al. 2011). In addition, I assumed that if bears are consuming anthropogenic foods in any capacity, they are also consuming some level of C_4 plants, either as agricultural corn or in human foods (Mizukami et al. 2005). This may be incorrect to assume, as fruit trees were found to be a major source of anthropogenic food for black bears in Montana (Merkle et al. 2013) and California (Greenleaf et al. 2009). I also assumed that the most likely C_4 plant available to bears in Vermont is corn, and that all C_4 plants available are anthropogenic in nature. Other potential anthropogenic sources of C_4 plants are sugarcane, sorghum, millet, and amaranth (Vogel and Merwe 1977). While there are some wild and invasive C_4 plants that may be found in Vermont, C_4 plants are rare in temperate climates (O'Rourke et al. 2010) and it is unlikely that these plants are substantial food sources (Narita et al. 2011).

I assumed that human hair is a reliable proxy for human diets, and therefore represents food items that black bears might consume from garbage. Samples from garbage may be more appropriate, although more difficult to homogenize. Likewise, I assumed that adult white-tailed deer hair would be an appropriate proxy for fawn isotope values. Although enrichment in $\delta^{15}N$ values has been documented in calves relative to adult cattle (Kohzu et al. 2009), Jenkins et al. (2001) found no trend of trophic enrichment between fawns and adult deer.

Collecting plants opportunistically was assumed to be an adequate way to summarize food source estimates for the entire range in which black bear hair samples were collected from. Although more systematic collection of plant food sources may have yielded a more complete coverage of the study area, stable isotope values in plants are highly variable between seasons, microhabitats, soil composition and other factors and may vary within tissues of an individual and among individuals of the same species. $\delta^{15}N$ values in particular are extremely variable as a result of factors such as isotopic routing, growth stage and environmental conditions (Evans 2001) and it may be incorrect to assume that the isotopic values of a single plant tissue reflects the isotopic composition of the entire plant or species (Szpak et al. 2012b). Therefore, estimating the exact isotopic values of food sources may be impossible, and the best alternative may be to represent the range of possible values. Additionally, my food source isotope values suggest that it may be critical to establish site relevant isotope baselines (Tykot 2004). Finally, an assumption was made that modern food samples would have comparable values to foods consumed during the years in which bear samples were collected. I did not apply a Suess effect correction of -0.022‰ per year to samples to account for global

decrease of ^{13}C in atmospheric CO_2 as a result of fossil fuel burning, as other studies have done (Hopkins and Ferguson 2012), because this would require an assumption that all food sources are influenced in the same way by atmospheric CO_2.

Other assumptions that may have influenced results relate to methods used to analyze contribution of food items to diet. The use of non-informative priors, estimated discrimination factors and estimated concentration values are all potential sources of error. The interpretation of stable isotope data is absolutely dependent on an in depth understanding of nutritional ecology (Hobson et al. 2000), and due to the impossibility of measuring all of these parameters for each unique study scenario, many assumptions must be made. In addition, the mixing space was assumed to have adequate geometry, an essential component for mixing models (Phillips et al. 2014), and Deviance Information Criterion (DIC) was assumed to be an adequate measure of model fit, despite criticisms that it can result in overfitting the observed data (Ando 2010). Finally, the negative correlation between C_3 plants and corn observed in the joint posterior plot (Figure A-5.7), indicates an unavoidable model inadequacy where the two source signals have opposing isotopic source signatures and when one is at the top of its posterior probability range, the other is likely to be a the bottom of its range. The negative correlation between human food and corn is a result of similar source signals in which both cannot be at the top of their posterior distribution ranges at the same time. Model uncertainly, therefore is artificially inflated and when it is impractical to combine source proportions a posteriori, there is no way to reduce this uncertainty (Phillips et al. 2014). The complexity of the physiological processes, stoichiometry, isotopic discrimination, and nutritional ecology that influence the isotopic values of sources and consumers leads to a vast number of

parameters that must be measured, estimated or assumed. Caution should be used when using posterior proportional contribution estimates to inform management decisions and continued efforts to analyze these inputs via controlled experiments and studies of wild animals will lead to greater ability to apply these methods to diet studies.

Stable isotope analysis using Bayesian mixing models has the potential to provide a non-invasive, flexible, and powerful means by which to estimate proportional contributions to diet over a range of time periods using a variety of tissues. Analysis of stable isotopes for diet reconstruction may provide insights into relationships between consumers and food sources that would be difficult or impossible to quantify via traditional diet analysis methods. These methods will be most useful when used in combination with traditional methods of diet analysis to provide a more complete picture of diet and to control for any inherent inadequacies.

Results from this analysis suggest that black bears in Vermont are primarily herbivorous with a diet consisting of mainly C_3 plants and consume C_4 plants, likely in the form of corn, as the second largest dietary source. Animal tissue contributed less to diet than in some other areas of black bear range, which is consistent with assumptions made about black bear foraging habits in Vermont. Nuisance bears exhibit more variability in their range of posterior proportional contributions to diet, and may forage more on corn and human foods and less on C_3 plants than the general population. This is expected given that nuisance bears subject to lethal management are often food-conditioned.

Black bears are dependent on a wide range of natural foods in Vermont, and the results of this study provide support for the importance of maintaining natural plant food

sources for black bears. Limiting the loss of existing hard mast stands and increasing the use of forestry practices that favor mast producing species and disturb soil in a way that promotes growth of top contributors to diet such as jewelweed and tall nodding sedge may increase the availability of natural plant food sources. Preserving adequate habitat in which black bears can forage for these natural food items may, likewise, support black bears in maintaining a diet high in these natural sources of food. Although corn is likely to continue being an important supplemental food source for black bears, these actions may limit the need for bears to forage on anthropogenic food sources and as a result contribute towards reducing the rate of human-bear conflict in Vermont.

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3.9 Figure Legends

Figure 3.1. Map of study area showing plant sample collection sites, number of bear hair samples collected from towns, and human hair sample collection site. Deer hair samples were collected in each county.

Figure 3.2. Distribution of uncorrected $\delta^{13}C$ and $\delta^{15}N$ values of black bears and four potential food groups in Vermont.

Figure 3.3. Mean ± 1SD isotope values for bear hair samples (●) and four food source groups. $\delta^{13}C$ and $\delta^{15}N$ are corrected for trophic discrimination. Mean source values are represented by points where error bars (1 SD) cross.

Figure 3.4. Posterior density estimates of diet source contributions to black bears killed for nuisance behavior in Vermont.

Figure 3.5. Posterior density estimates of diet source contributions to black bears with no known record of nuisance behavior in Vermont.

3.10 Tables

Table 3.1. Hair growth years determined by month in which hairs were collected from studies examining bear diet through stable isotope analysis.

	Hair Growth Period		
	Previous Year	**Current Year**	**Excluded from Study**
Felicetti et al. (2003)	May to mid-June	September-Nov	Late-June through August
Ben-David et al. (2004)	June-July		
Mizukami et al. (2005)	May-June	August-Fall	July
Jones et al. (2006)	Before July 2nd		
Hopkins and Ferguson (2012)	Spring and early summer	Late summer and fall	
Fortin et al. (2013)	Before mid-August		Mid-August and later
Bentzen et al. (2014)	Spring-July	August-Fall	
Hopkins et al. (2014b)	May-August	September-onward	
Schwartz et al. (2014)	May-June	August-October	July
Teunissen van Manen et al. (2014)	May-August		

Table 3.2. Covariate names, descriptions and types used in models to describe bear diet. Data sources are listed.

Covariate Name	Description	Covariate Type	Source
Status	Nuisance Status as determined by cause of death. All causes of death other than nuisance are considered to be "non-nuisance"	Categorical	Vermont Fish and Wildlife Department (VFWD) Bear Sample Records: C.W. Kilpatrick Lab
Sex	Determined by individuals when collecting hair samples	Categorical	VFWD Bear Sample Records: C.W. Kilpatrick Lab
Beech	Beech Hard Mast Production Rating (HMPR) categorized as: excellent, good, fair and poor. Based on average nuts/plot at sample sites in a given year.	Categorical	VFWD Mast Report 2010
Oak	Oak HMPR categorized as: excellent, good, fair and poor. Based on average nuts/plot at sample sites in a given year.	Categorical	VFWD Mast Report 2010
Agriculture	% Agriculture calculated from NLCD Class #: 81,82	Continuous	National Land Cover Database (NLCD) 2001 v. 2011
Cultivated	% Cultivated calculated from NLCD Class #: 82	Continuous	NLCD 2001 v. 2011
Developed	% Developed calculated from NLCD Class #: 21,22,23,24	Continuous	NLCD 2001 v. 2011
Forest	% Forest calculated from NLCD Class #: 41,42,43	Continuous	NLCD 2001 v. 2011
Agriculture/Developed	% Agricultural and Developed calculated as %Agriculture + % Developed	Continuous	NLCD 2001 v. 2011

Table 3.3. Mean raw isotope values (‰), discrimination factors (‰), elemental concentrations (%) and concentrations incorporating digestibility (%) of food sources. Standard deviation reported in parentheses.

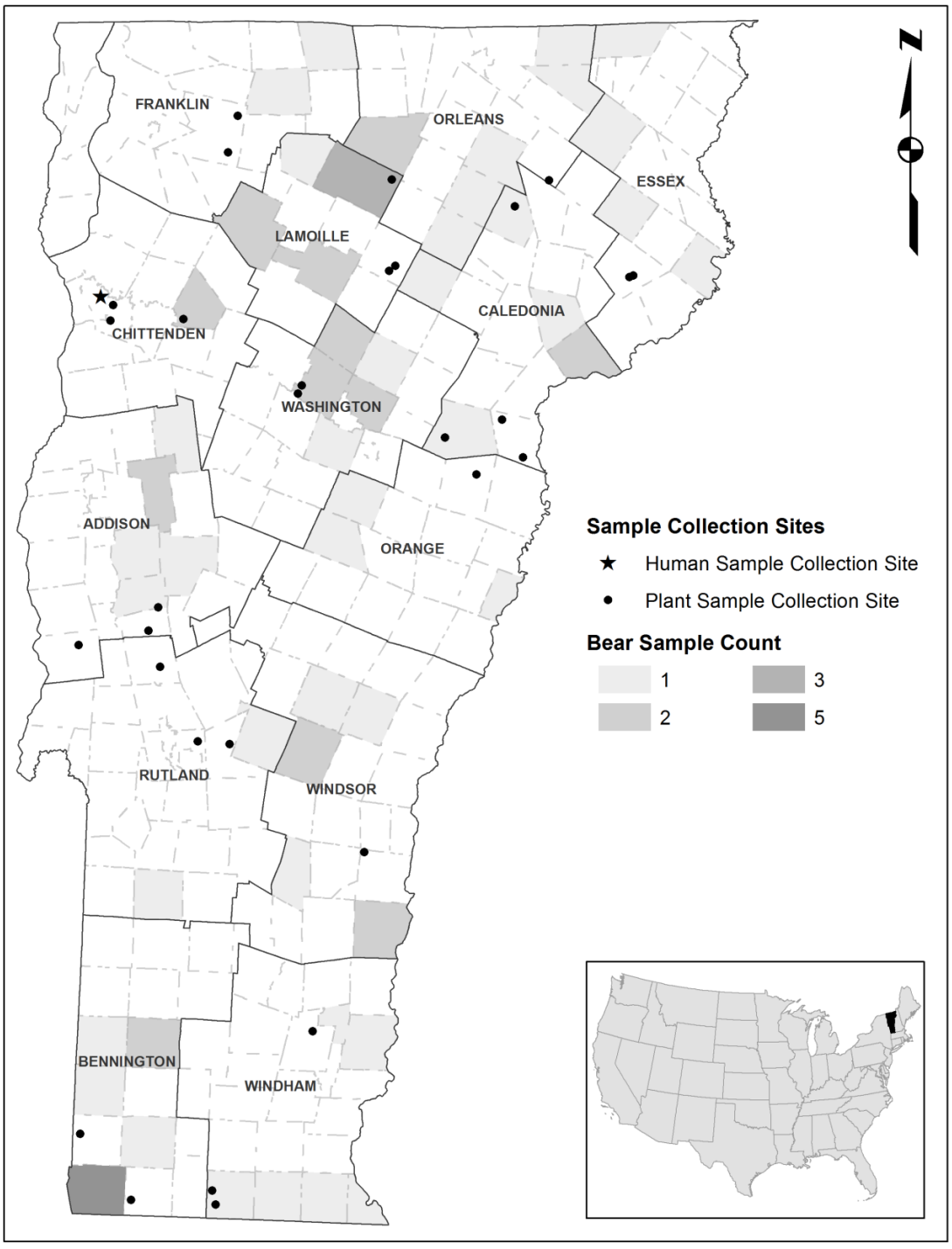
Food Sources	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\Delta^{13}C$ (‰)	$\Delta^{15}N$ (‰)	[C] (%)	[N] (%)	Digest [C] (%)	Digest [N] (%)
C_3 Plants	121	-30.81 (2.65)	-0.82 (2.31)	3.00 (1.27)	4.25 (0.78)	45.86 (2.70)	1.86 (0.61)	46.50 (3.77)	3.50 (2.28)
Corn	12	-11.61 (0.48)	6.43 (3.38)	3.00 (1.27)	4.25 (0.78)	46.48 (0.00)	2.19 (0.00)	45.77 (0.00)	1.97 (0.00)
Deer	38	-25.66 (1.63)	4.49 (1.05)	3.10 (1.34)	3.91 (0.54)	53.13 (0.00)	13.87 (0.00)	53.13 (0.00)	13.87 (0.00)
Human	20	-17.50 (0.59)	8.53 (0.34)	0.00 (0.00)	0.00 (0.00)	53.48 (0.00)	7.11 (0.00)	52.83 (0.00)	6.88 (0.00)

Table 3.4. Summary of stable isotope mixing models explaining variation in black bear diets among several factors. Models could include one or two covariates, use two types of concentration dependency and be fixed or continuous. Yes (Y) and No (N) indicate whether models include individuals as random effects or residual error. Models are ranked according to data support (top models with the most support are in bold).

Model #	Model Name	Effect Type	Individual	Residual	Conc. Dep	DIC
17	Status	Fixed	N	Y	Digest	**2008.59**
22	Oak, Status	Fixed	N	Y	Digest	**2009.18**
31	Status, Sex	Fixed	N	Y	Digest	**2012.32**
33	Status, Beech	Fixed	N	Y	Digest	**2014.31**
23	Oak, Status	Fixed	Y	N	Digest	2061.18
16	Status	Fixed	Y	N	Digest	2062.83
32	Status, Beech	Fixed	Y	N	Digest	2065.17
30	Status, Sex	Fixed	Y	N	Digest	2066.80
35	Status, Agriculture	Status; Continuous	Y	N	Digest	2069.603
37	Status, Agriculture/Developed	Fixed; Continuous	Y	N	Digest	2070.27
36	Status, Developed	Status; Continuous	Y	N	Digest	2070.374
34	Status, Forest	Fixed; Continuous	Y	N	Digest	2077.17
1	Null	N/A	N	Y	Digest	2110.10
6	Beech	Fixed	N	Y	Digest	2111.60
14	Sex	Fixed	N	Y	Digest	2111.83
7	Oak	Fixed	N	Y	Digest	2112.29
20	Beech, Sex	Fixed	N	Y	Digest	2113.24
25	Oak, Sex	Fixed	N	Y	Digest	2113.82
18	Beech, Oak	Fixed	N	Y	Digest	2116.83
2	Null	N/A	N	Y	Element	2126.30
4	Null	N/A	Y	N	Element	2173.91
5	Beech	Fixed	Y	N	Digest	2178.30
8	Oak	Fixed	Y	N	Digest	2179.08
28	Oak, Agriculture/Developed	Fixed; Continuous	Y	N	Digest	2186.562
3	Null	N/A	Y	N	Digest	2187.67
24	Oak, Sex	Fixed	Y	N	Digest	2188.80
15	Sex	Fixed	Y	N	Digest	2188.82
12	Agriculture/Developed	Continuous	Y	N	Digest	2190.49
44	Beech, Developed	Fixed; Continuous	Y	N	Digest	2190.669
27	Oak, Developed	Fixed; Continuous	Y	N	Digest	2191.09
19	Beech, Oak	Fixed	Y	N	Digest	2192.24
10	Developed	Continuous	Y	N	Digest	2192.89
42	Beech, Agriculture/Developed	Fixed; Continuous	Y	N	Digest	2193.10
21	Beech, Sex	Fixed	Y	N	Digest	2193.24
9	Forest	Continuous	Y	N	Digest	2195.00
11	Agriculture	Continuous	Y	N	Digest	2196.25
13	Cultivated	Continuous	Y	N	Digest	2196.63
26	Oak, Forest	Fixed; Continuous	Y	N	Digest	2198.62
29	Oak, Forest	Fixed; Continuous	Y	N	Digest	2198.618
43	Beech, Forest	Fixed; Continuous	Y	N	Digest	2199.791
45	Beech, Agriculture	Fixed; Continuous	Y	N	Digest	2201.58

Model #	Model Name	Effect Type	Individual	Residual	Conc. Dep	DIC
41	Sex, Agriculture/Developed	Fixed; Continuous	Y	N	Digest	2202.04
39	Sex, Agriculture	Fixed; Continuous	Y	N	Digest	2202.568
38	Sex, Forest	Fixed; Continuous	Y	N	Digest	2202.695
40	Sex, Developed	Fixed; Continuous	Y	N	Digest	2202.759

3.11 Figures



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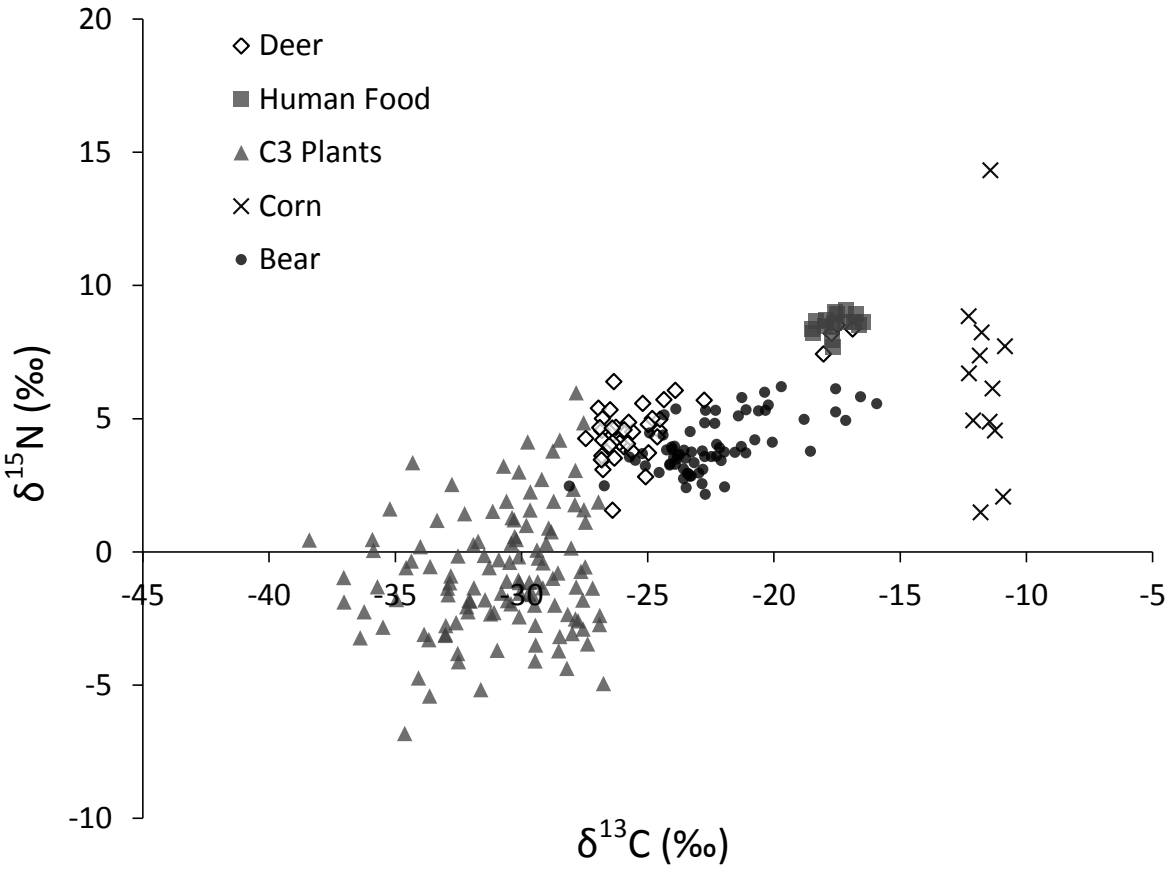

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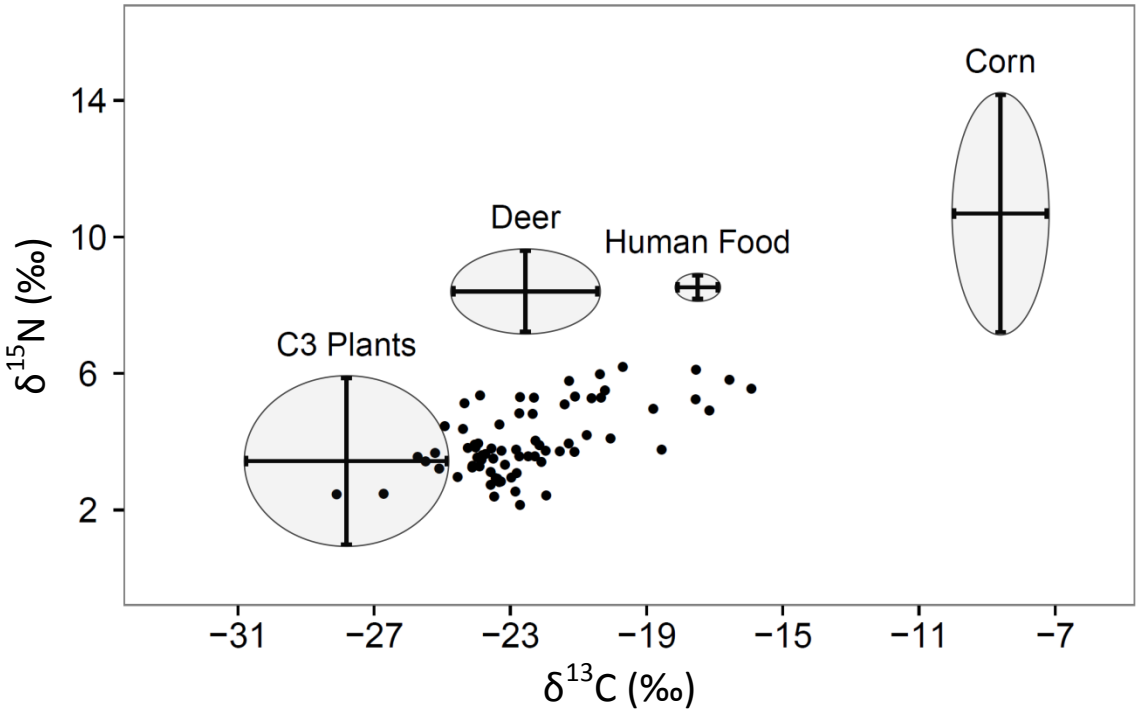

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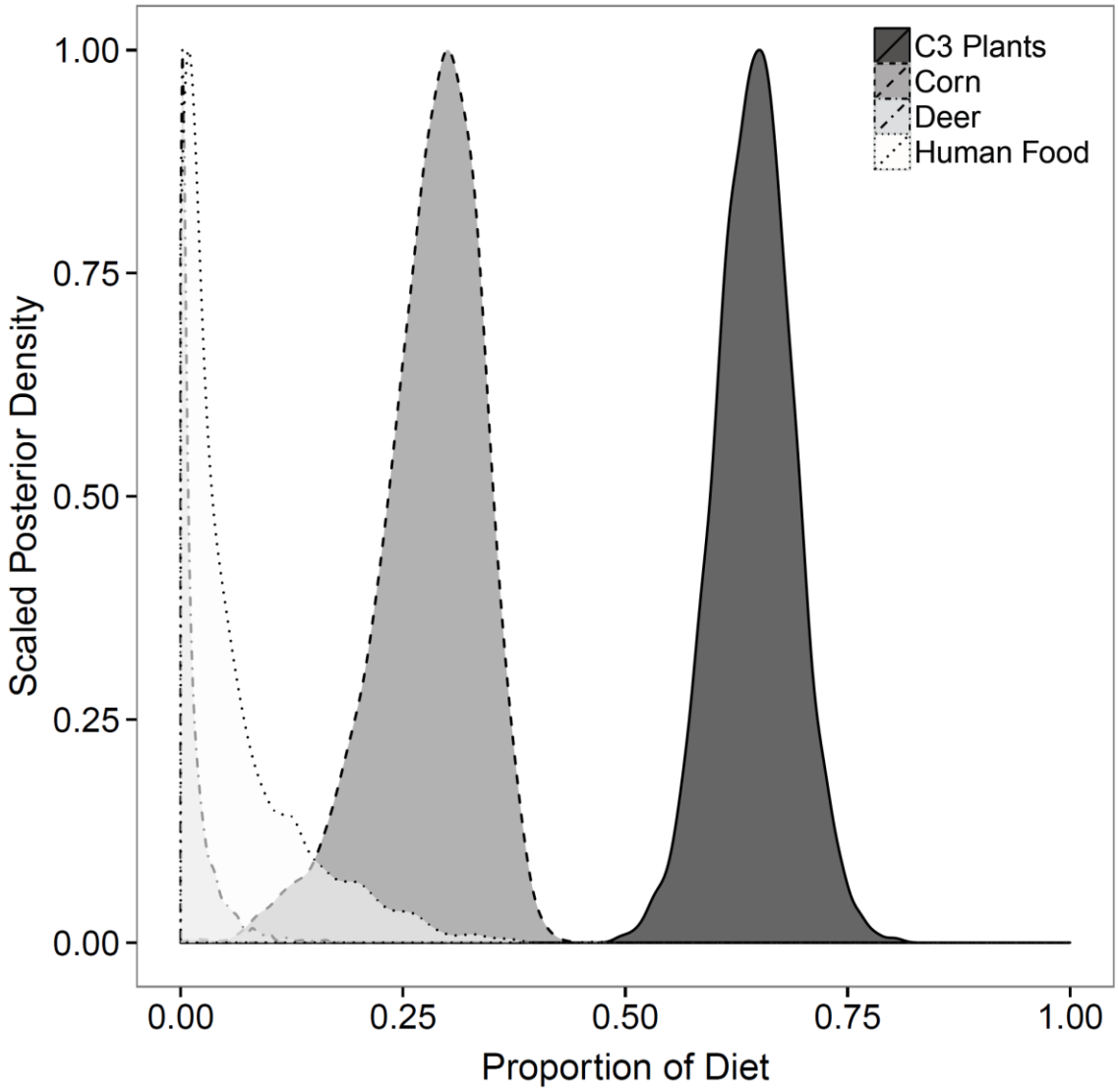

Figure 3.4. Posterior density estimates of diet source contributions to black bears killed for nuisance behavior in Vermont.

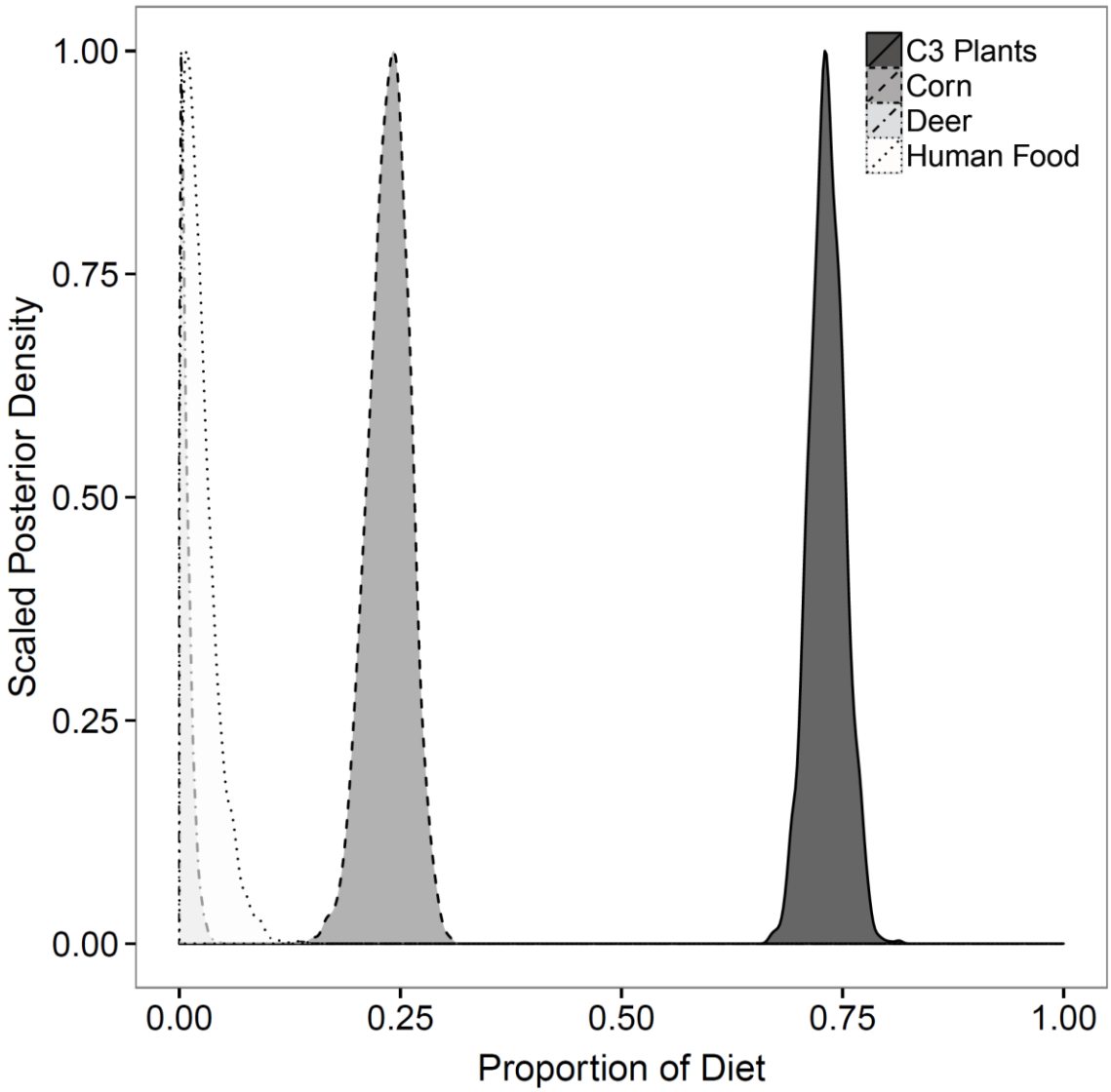

Figure 3.5. Posterior density estimates of diet source contributions to black bears with no known record of nuisance behavior in Vermont.

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CHAPTER 5: APPENDICES

5.1 Appendix A: Tables

Table A-5.1. Mann-Whitney *U* test scores for tests of significant difference between $\delta^{13}C$ and $\delta^{15}N$ values of black bear diet sources. Human hair samples represent human diet.

Diet Source	N		C_3 plants	Corn	White-tailed deer	Human
C_3 plants	121	$\delta^{13}C$		0^{***}	18^{***}	0^{***}
		$\delta^{15}N$		38^{***}	120^{***}	0^{***}
Corn	12	$\delta^{13}C$	0^{***}		456^{***}	240^{***}
		$\delta^{15}N$	38^{***}		337^{*}	41^{**}
Deer	38	$\delta^{13}C$	18^{***}	456^{***}		3^{***}
		$\delta^{15}N$	120^{***}	337^{*}		0^{***}
Human	20	$\delta^{13}C$	0^{***}	240^{***}	3^{***}	
		$\delta^{15}N$	0^{***}	41^{**}	0^{***}	

*, **, *** indicate isotope values are statistically different at the 0.05, 0.01, and 0.001 significance levels, respectively.

Table A-5.2. Average trophic discrimination values ($\Delta^{13}C$ (‰) and $\Delta^{15}N$ (‰)) calculated from values used in studies that evaluated bear diet and foraging behavior through stable isotope analysis. Sources ordered by publication date.

			Discrimination Factors		$\Delta^{13}C$ (‰)		$\Delta^{15}N$ (‰)	
Source	**Species**	**Type**	**$\Delta^{13}C$ (‰)**	**$\Delta^{15}N$ (‰)**	**Meat**	**Plants**	**Meat**	**Plants**
Hilderbrand et al. (1996)	Black Bear	Blood	0.4 to 4.5	4.1 ± 0.8	2.45	2.45	4.1	4.1
Hobson et al. (2000)	Brown Bear, Black Bear	Hair	Not Provided	Equation[a]	N/A	N/A	Equation	Equation
Phillips and Koch (2002)	Black Bear/Brown Bear	Hair	Meat: 4.9[b] Plants: 3.3[b]	Meat: 4.0[b] Plants: 4.1[b]	4.9	3.3	4	4.1
Felicetti et al. (2003)	Brown Bear	Blood	Too Variable	3.2 - 5.0	N/A	N/A	4.1	4.1
Ben-David et al. (2004)	Brown Bear	Hair	2[c]	3[d]	2	2	3	3
Greenleaf (2005)	Black Bear	Hair	6[e]	3.5[f]	6	6	3.5	3.5
Mowat and Heard (2006)	Brown Bear	Hair	2[g]	Meat: 5.0 ± 1[h] Plants: 5.6 ± 3[h]	2	2	5	5.6
Fortin et al. (2007)	Brown Bear/Black Bear	Hair	3.7 ± 1.3[i]	Equation[h]	3.7	3.7	Equation	Equation
Merkle et al. (2011)	Black Bear	Hair	2 ± 1[j]	4.1 ± 0.45[k]	2	2	4.1	4.1
Narita et al. (2011)	Brown Bear	Liver	2[l]	Meat: 4[l] Plants: 5[l]	2	2	4	5
Hopkins and Ferguson (2012)	Black Bear	Hair	Equation[m]	Equation[m]	Equation	Equation	Equation	Equation
Hopkins et al. (2012)	Black Bear	Hair	N/A	N/A	N/A	N/A	N/A	N/A
Van Daele et al. (2013)	Brown Bear	Hair	3.7 ± 0.2[n]	Meat: 4.0 ± 0.5[o] Plants: 5.2 ± 0.5[o]	3.7	3.7	4	5.2
Fortin et al. (2013)	Brown Bear/Black Bear	Hair	N/A N/A	Meat: 4.0 ± 0.1[p] Plants: 4.5 ± 0.5[p]	N/A	N/A	4	4.5
Milakovic and Parker (2013)	Brown Bear	Hair	3.9 ± 0.13[k]	4.5 ± 0.32[k]	3.9	3.9	4.5	4.5
Hopkins et al. (2014a)	Black Bear	Hair	2.5 ± 0.9[q]	3.4 ± 1.2[q]	2.5	-	3.4	-
Schwartz et al. (2014)	Brown Bear	Hair, Blood	N/A N/A	Meat: 4.0 ± 0.1[p] Plants: 4.5 ± 0.5[p]	N/A	N/A	4	4.5
Teunissen van Manen et al. (2014)	Black Bear	Hair	2[r]	3[r]	2	2	3	3
				Average (1 SD)	3.10 (1.34)	3.00 (1.27)	3.91 (0.54)	4.25 (0.78)

[a] Equation from Hilderbrand et al. (1996).
[b] From Hilderbrand et al. (1996) Δ values determined for bear blood for bears fed mule deer and apples. Incorporates fractionation and substrate-routing effects, may use 0.5‰ error.
[c] Ben-David (1996), Ben-David and Schell (2001), Hilderbrand et al. (1996)
[d] Ben-David (1996), Hilderbrand et al. (1996)
[e] Drawing from results of Felicetti et al. (2003)
[f] Based on DeNiro and Epstein (1978), Hobson and Clark (1992), Hobson and Schell (1998), Kelly (2000) Ben-David et al. (1997b), Hilderbrand et al. (1996), Felicetti et al. (2003)
[g] Ben-David et al. (2004)
[h] Equation from Felicetti et al. (2003)
[i] Average for all foods from Hilderbrand et al. (1996), Ben-David and Schell (2001), Felicetti et al. (2003)
[j] Value taken from Mowat and Heard (2006), Ben-David et al. (2004)
[k] Mean discrimination values taken from Hilderbrand et al. (1996), generated from models created from captive bears
[l] Based on data from Hilderbrand et al. (1996); Felicetti et al. (2003); Robbins et al. (2005) and Ben-David et al. (2004)
[m] Equation from Kurle (2008), results in some negative discrimination factor values
[n] Fortin et al. (2007)
[o] Felicetti et al. (2003); Robbins et al. (2005); Fortin et al. (2007); Florin et al. (2011)
[p] Robbins et al. (2005) and Florin et al. (2011)
[q] Mean diet-hair discrimination values taken from Caut et al. (2009), only used to adjust trout values, did not apply to other plants and animals, instead assumed used values from bears only eating plants and animals and human hair.
[r] Values are average of values used in similar isotopic studies (See Table 4 in Teunissen Van Manen (2011)).

Table A-5.3. Isotope values ($\delta^{13}C$ and $\delta^{15}N$) and covariates for black bears killed in Vermont, 1998-2005. Hunter, road and starvation caused deaths were assumed to have "Non-nuisance" status for this study. Percent land cover types were calculated using the National Land Cover Database 2001 v. 2011 from USGS (Jin et al. 2013). Beech and Oak hard mast ratings (HMPR) came from surveys conducted by the Vermont Fish and Wildlife Department (Hammond 2010).

ID	Town	% Developed	% Forest	% Ag	% Cultivated	Date Killed	Hair Year	Beech HMPR	Oak HMPR	Kill Type	Sex	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
190	Sheffield	5.7	75.1	10.9	4.7	10/3/1999	1999	Poor	Poor	Road	M	-24.6	3.0
243	Middlesex	7.0	79.0	9.1	3.2	11/4/2000	2000	Excellent	Good	Road	M	-21.3	5.8
244	Worcester	5.6	78.1	10.6	3.8	11/11/2000	2000	Excellent	Good	Road	M	-23.6	3.1
245	Pownal	7.8	74.2	11.5	1.1	11/11/2000	2000	Excellent	Good	Hunter	M	-22.3	3.6
246	East Haven	2.3	83.8	3.0	1.8	11/13/1999	1999	Poor	Poor	Hunter	F	-23.4	2.9
247	Eden	3.4	81.2	9.2	3.6	11/13/1999	1999	Poor	Poor	Hunter	F	-20.3	5.3
251	Springfield	8.4	77.1	9.5	1.6	11/14/1999	1999	Poor	Poor	Hunter	M	-23.8	3.6
252	Halifax	5.4	82.6	7.4	0.2	11/14/1999	1999	Poor	Poor	Hunter	M	-22.0	3.7
256	Barnard	4.8	83.6	7.9	0.6	4/14/2001	2000	Excellent	Good	Starvation	F	-24.0	3.5
262	Arlington	4.4	75.0	13.6	2.8	10/6/2001	2001	Poor	Excellent	Road	F	-22.3	4.0
265	Guilford	7.3	78.9	8.3	1.2	8/27/2001	2001	Poor	Excellent	Road	M	-23.2	3.3
313	Killington	5.5	86.7	3.6	0.2	10/11/2001	2001	Poor	Excellent	Road	F	-28.1	2.5
443	Worcester	5.6	78.1	10.6	3.8	7/9/2003	2002	Excellent	Fair	N/A	F	-23.3	3.8
447	Danby	3.1	78.4	11.6	1.6	10/6/2003	2003	Poor	Poor	N/A	F	-21.6	3.7
448	Berlin	9.0	73.3	12.5	5.0	10/3/2003	2003	Poor	Poor	N/A	F	-22.2	3.9
187	Lowell	3.4	79.1	11.3	4.3	10/7/1999	1999	Poor	Poor	Road	M	-25.2	3.7
189	East Montpelier	8.3	74.2	11.3	5.2	10/3/1999	1999	Poor	Poor	Hunter	M	-25.7	3.6
456	Starksboro	3.5	74.3	16.8	3.3	1/17/2004	2003	Poor	Poor	Nuisance	M	-20.4	6.0
457	Jericho	9.3	72.1	13.0	3.5	7/16/2004	2003	Poor	Poor	Road	M	-24.4	5.1
459	Cambridge	4.6	79.0	12.2	3.5	9/4/2004	2004	Fair	Poor	Road	F	-20.1	4.1
461	Middlebury	4.2	51.0	33.1	9.6	10/12/2004	2004	Fair	Poor	Road	M	-25.5	3.4
462	Ludlow	4.3	84.5	6.4	0.2	9/23/2005	2005	Poor	Good	Road	M	-23.9	3.3
463	Guildhall	3.6	77.7	5.2	3.7	10/13/2005	2005	Poor	Good	Road	F	-21.1	3.7

ID	Town	% Developed	% Forest	% Ag	% Cultivated	Date Killed	Hair Year	Beech HMPR	Oak HMPR	Kill Type	Sex	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
464	Westminster	6.0	80.0	9.3	2.1	6/14/2005	2004	Fair	Poor	Nuisance	F	-23.3	4.5
465	Springfield	8.4	77.1	9.5	1.6	9/2/2004	2004	Fair	Poor	Road	M	-26.7	2.5
466	Woodford	4.8	80.4	6.0	0.3	9/2/2004	2004	Fair	Poor	Hunter	F	-23.9	5.4
467	Pownal	7.8	74.2	11.5	1.1	5/15/2005	2004	Fair	Poor	Nuisance	M	-22.3	5.3
469	Bridgewater	3.8	87.1	6.3	0.3	10/1/2005	2005	Poor	Good	Road	M	-25.1	3.2
470	Bridgewater	3.8	87.1	6.3	0.3	8/12/2005	2005	Poor	Good	Road	M	-24.9	4.5
471	Pownal	7.8	74.2	11.5	1.1	4/28/2005	2004	Fair	Poor	Nuisance	M	-20.6	5.3
473	Whitingham	4.2	85.2	4.9	0.2	11/16/2004	2004	Fair	Poor	Hunter	M	-24.4	4.4
474	Fairlee	5.5	79.5	9.3	3.9	12/16/2000	2000	Excellent	Good	Road	M	-17.6	5.3
476	Pownal	7.8	74.2	11.5	1.1	11/14/1998	1998	Excellent	Good	Hunter	M	-22.8	3.8
477	Pownal	7.8	74.2	11.5	1.1	10/13/2004	2004	Fair	Poor	Hunter	F	-20.2	5.5
478	Bristol	4.4	64.2	24.7	5.8	12/16/2000	2000	Excellent	Good	Road	M	-22.4	4.8
479	Cambridge	4.6	79.0	12.2	3.5	10/10/2000	2000	Excellent	Good	Road	M	-17.6	6.1
481	Waterford	7.2	74.8	8.6	3.4	11/14/1998	1998	Excellent	Good	Hunter	M	-16.6	5.8
482	Hardwick	4.1	77.3	10.3	4.7	11/15/1998	1998	Excellent	Good	Hunter	M	-23.3	2.8
483	Belvidere	3.2	82.9	9.1	3.1	11/14/1998	1998	Excellent	Good	Hunter	F	-23.3	2.9
484	Eden	3.4	81.2	9.2	3.6	11/14/1998	1998	Excellent	Good	Hunter	M	-23.5	3.5
485	Holland	4.6	70.0	12.2	4.7	11/14/1998	1998	Excellent	Good	Hunter	F	-22.7	3.6
486	Brighton	2.2	82.0	2.3	1.0	11/14/1998	1998	Excellent	Good	Hunter	M	-22.9	2.6
487	Norton	1.6	83.2	3.6	1.7	11/14/1998	1998	Excellent	Good	Hunter	F	-23.0	3.0
488	Morgan	4.7	70.6	9.5	3.6	11/15/1998	1998	Excellent	Good	Hunter	M	-24.1	3.9
489	Greensboro	4.5	75.2	12.1	4.9	11/14/1998	1998	Excellent	Good	Hunter	M	-21.1	5.3
490	Glover	5.1	72.2	13.7	5.0	11/14/1998	1998	Excellent	Good	Hunter	F	-22.7	4.8
491	Jericho	9.3	72.1	13.0	3.5	11/14/1998	1998	Excellent	Good	Hunter	F	-22.7	2.2
492	Bristol	4.4	64.2	24.7	5.8	11/15/1998	1998	Excellent	Good	Hunter	F	-23.4	3.0
493	Vernon	8.3	75.6	8.7	1.8	11/14/1998	1998	Excellent	Good	Hunter	F	-22.0	2.4

ID	Town	% Developed	% Forest	% Ag	% Cultivated	Date Killed	Hair Year	Beech HMPR	Oak HMPR	Kill Type	Sex	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
231	Sunderland	3.5	83.8	4.3	0.3	11/11/2000	2000	Excellent	Good	Hunter	M	-22.5	3.6
248	Eden	3.4	81.2	9.22	3.6	11/13/1999	1999	Poor	Poor	Hunter	M	-21.3	4.0
249	Lowell	3.4	79.1	11.26	4.3	11/14/1999	1999	Poor	Poor	Hunter	M	-18.8	5.0
257	Groton	5.3	78.5	9.34	4.3	6/30/2001	2000	Excellent	Good	Nuisance	M	-23.6	3.8
258	Enosburg	4.3	66.5	22.82	6.1	6/28/2001	2000	Excellent	Good	Nuisance	M	-22.7	5.3
260	Waterford	7.2	74.8	8.64	3.4	6/14/2001	2000	Excellent	Good	Nuisance	M	-21.4	5.1
263	Richford	4.1	75.9	16.16	5.3	9/29/2001	2001	Poor	Excellent	Hunter	M	-24.1	3.3
312	Ripton	3.5	77.1	11.44	2.3	11/10/2001	2001	Poor	Excellent	Hunter	M	-24.0	3.8
458	St. Johnsbury	7.1	74.5	11.86	4.6	9/29/2004	2004	Fair	Poor	Nuisance	M	-19.7	6.2
468	Shaftsbury	6.1	69.7	16.12	2.5	9/4/2005	2005	Poor	Good	Road	M	-15.9	5.6
480	Athens	5.0	84.2	6.51	0.9	11/14/1998	1998	Excellent	Good	Hunter	M	-23.6	2.8
494	Willamstown	8.2	75.2	11.27	5.4	11/14/1998	1998	Excellent	Good	Hunter	M	-24.1	3.3
440	Sunderland	3.5	83.8	4.29	0.3	5/14/2003	2002	Excellent	Fair	N/A	M	-20.8	4.2
441	Calais	4.7	79.8	9.58	4.3	9/5/2003	2003	Poor	Poor	N/A	M	-18.6	3.8
442	Middlesex	7.0	79.0	9.11	3.2	8/10/2003	2003	Poor	Poor	N/A	M	-23.8	3.5
445	Brookfield	6.0	76.3	12.88	5.4	7/12/2003	2002	Excellent	Fair	N/A	M	-24.3	3.8
446	Morristown	5.4	79.4	10.38	3.6	7/6/2003	2002	Excellent	Fair	N/A	M	-22.8	3.1
449	Morristown	5.4	79.4	10.38	3.6	6/17/2003	2002	Excellent	Fair	N/A	M	-22.1	3.4
450	East Montpelier	8.3	74.2	11.28	5.2	7/6/2003	2002	Excellent	Fair	N/A	M	-17.2	4.9
451	Salisbury	4.1	51.5	28.87	7.9	10/1/2003	2003	Poor	Poor	N/A	M	-23.5	2.4
452	Pomfret	5.8	80.3	10.51	0.8	8/28/2003	2003	Poor	Poor	N/A	M	-23.7	3.7
453	Barton	5.6	69.3	15.38	6.0	8/25/2003	2003	Poor	Poor	N/A	M	-23.9	4.0

Table A-5.4. Digestibility and concentration calculations for sampled C_3 plants (excluding acorns and beechnuts). Calculations were made using the equations from Hopkins and Ferguson (2012). Digest DM is digestibility of dry matter, [C] and [N] are elemental concentrations.

	Data from Samples						Concentrations (%)			
	%N	%C	C/N	Digest DM	Digest N	Digest C	Digest [N]	Digest [C]	[N]	[C]
Jack-in-the-Pulpit	1.4	41.5	31.8	57.8	1.3	26.0	2.2	45.0	1.4	41.5
Sedge	2.0	46.1	23.4	35.0	1.8	15.8	5.2	45.0	2.0	46.1
Blackberry	2.2	46.9	21.8	63.4	1.9	28.5	3.1	45.0	2.2	46.9
Raspberry	2.1	47.7	24.2	63.4	1.9	28.5	2.9	45.0	2.1	47.7
Jewelweed	2.8	42.1	15.2	35.0	2.5	15.8	7.1	45.0	2.8	42.1
Cherry (fruit)	1.6	50.4	32.0	63.4	1.4	28.5	2.2	45.0	1.6	50.4
Cherry (leaves)	2.7	46.0	17.1	35.0	2.4	15.8	6.9	45.0	2.7	46.0
Beech (leaf)	2.8	48.4	17.6	35.0	2.5	15.8	7.1	45.0	2.8	48.4
Oak (leaf)	2.7	48.6	17.9	35.0	2.5	15.8	7.0	45.0	2.7	48.6
Apple	1.3	44.1	35.3	63.4	1.1	28.5	1.8	45.0	1.3	44.1

Equations from Hopkins and Ferguson (2012):
% protein = % N x 6.25
Digest DM = compiled mean data (Robbins et al. (2002) *cited in* Hopkins and Ferguson (2012))
Digest N (plants) = % N x 0.9 (assuming 90% of % N is digestible)
Digest C (plants) = Digest DM x 0.45 (assuming Digest DM is 45% C for fruit and leafy plants; Koch and Phillips (2002) *cited in* Hopkins and Ferguson (2012)
Digest [N] = (Digest N/Digest DM) x100
Digest [C] = (Digest C/Digest DM) x100

From Pritchard and Robbins (1990):
Digest DM (Jack-in-the-pulpit) = 57.80

Table A-5.5. Concentration values for human food, deer, corn and hard mast. Stoichiometric measurements were located on the USDA National Nutrient Database (U.S. Department of Agriculture: Agricultural Research Service 2014). Equations from Hopkins and Ferguson (2012).

	Units = gm/100 gm wet weight							Units = decimal % dry weight										Concentrations %		
	Water	Protein	Lipid	Carb	Ash	Total	Dry Total	Protein	Lipid	Carb	Ash	Protein N	Protein C	Lipid C	Carb C	Digest Protein C	Digest [N]	Digest [C]	[N]	[C]
Human Food[1]																	6.9	52.8	7.1	53.5
Deer[1,2]	75.0	21.5	2.7	0.0	0.6	99.8	24.8	0.9	0.1	0.0	0.0	0.1	0.5	0.1	0.0	0.5	13.9	53.1	13.9	53.1
Corn[1,3]	76.1	3.3	1.4	18.7	0.6	100.0	23.9	0.1	0.1	0.8	0.0	0.0	0.1	0.0	0.4	0.1	2.0	45.8	2.2	46.5
Beech (nut)[5]	6.6	6.2	50.0	33.5	3.7	100.0	93.4	0.1	0.5	0.4	0.0	0.0	0.0	0.4	0.2	0.0	0.5	57.9	1.1	48.0
Oak (acorn)[4]	27.9	6.2	23.9	40.8	1.4	100.0	72.1	0.1	0.3	0.6	0.0	0.0	0.0	0.3	0.3	0.0	0.6	52.3	0.9	45.2

[1] From: Hopkins and Ferguson (2012)
[2] NDB #35080 Venison
[3] NDB #11167 Corn
[4] NDB #12058 Acorns
[5] NDB # 12077 Beechnuts
[6] Robbins (1993)
[7] Mealey (1980)

Equations from Hopkins and Ferguson (2012):

Factors for calculating macronutrient dry weight (Robbins 1993):

Protein N = Protein (% dry weight) x 0.16
Protein C = Protein (% dry weight) x 0.52
Lipid C = Lipid (% dry weight) x 0.75
Carbohydrate C = Carbohydrate (% dry weight) x 0.45

Assume 100% digestibility for all sources for Lipid C and Carbohydrate C
Assume 100% protein digestibility for meat foods (Koch and Phillips 2002)
Assume 90% for plant foods (Koch and Phillips 2002)

Digest Protein C (meat) = Protein C x 1.0
Digest Protein C (corn) = Protein C x .90
Digest [C] = Digest Protein C + Lipid C + Carb C
Digest [N] (meat) = Protein N x 1.0 x 100
Digest [N] (corn) = Protein N x .90 x 100
Digest [N] (acorns, beech nuts) = (% protein dry weight (from NDB) x 0.16 N[6] x 0.466 (digestibility of pinenuts[7]))
Digest [C] (acorns, beech nuts) = (% protein dry weight (from NDB) x 0.52 C[6] x 0. 466 (digestibility of pinenuts[7])) + (% lipid dry weight x 0.75 C (100% digestible[6]) + (% carbohydrate dry weight x 0.45 C (100% digestible[6]))
[C] = (Protein C + Lipid C + Carb C) x 100
[N] = (Protein N) x 100

Table A-5.6. Posterior mean, standard deviation, and quantiles of diet item percent contribution estimates for four base models (%). Model 1 used concentration dependence values incorporating digestibility (Digest [C] and [N], residual and process error. Model 2 used elemental concentrations ([C] and [N]), residual and process error. Model 3 used Digest [C] and [N], process error and individuals as random effects. Model 4 used [C] and [N], process error and individuals as random effects.

Food Source	Mean	SD	2.50%	5%	25%	50%	75%	95%	97.50%
Model 1									
C_3 Plants	71.9	1.7	68.6	69.1	70.8	71.9	73.0	74.6	75.1
Corn	25.6	2.0	21.2	22.0	24.4	25.8	27.0	28.7	29.4
Deer	0.6	0.6	0.0	0.0	0.2	0.4	0.9	1.8	2.2
Human Food	1.9	1.6	0.1	0.1	0.6	1.4	2.7	5.2	6.0
Model 2									
C_3 Plants	73.5	1.8	70.0	70.5	72.3	73.5	74.7	76.5	77.1
Corn	25.2	1.8	21.5	22.1	24.0	25.2	26.4	28.1	28.7
Deer	0.4	0.4	0.0	0.0	0.1	0.3	0.5	1.2	1.4
Human Food	0.9	0.9	0.0	0.0	0.3	0.6	1.3	2.6	3.3
Model 3									
C_3 Plants	72.1	1.8	68.6	69.1	70.8	72.0	73.3	75.1	75.7
Corn	25.4	2.0	21.0	22.0	24.1	25.6	26.8	28.7	29.2
Deer	0.6	0.6	0.0	0.0	0.2	0.5	0.9	1.8	2.1
Human Food	1.9	1.6	0.1	0.1	0.6	1.4	2.7	5.1	6.1
Model 4									
C_3 Plants	73.7	1.8	70.1	70.8	72.5	73.7	74.9	76.7	77.3
Corn	25.0	1.9	21.3	21.9	23.8	25.1	26.3	28.0	28.6
Deer	0.4	0.4	0.0	0.0	0.1	0.3	0.5	1.0	1.3
Human Food	0.9	0.8	0.0	0.0	0.3	0.6	1.3	2.5	3.0

Table A-5.7. Posterior mean, standard deviation, and quantiles of diet item percent contribution estimates for four top models and covariates (%).

Covariate Level	Food Source	Mean	SD	2.50%	5%	25%	50%	75%	95%	97.50%
					Model 17					
Nuisance	C_3 Plants	64.5	4.4	55.8	57.2	61.6	64.6	67.4	71.8	73.2
	Corn	28.0	5.9	13.7	17.0	24.8	28.9	32.2	36.1	37.3
	Deer	1.6	2.3	0.0	0.0	0.2	0.7	2.0	6.1	8.2
	Human Food	5.9	6.9	0.1	0.1	0.9	3.2	8.3	20.9	25.1
Non-nuisance	C_3 Plants	73.2	2.0	69.3	70.1	71.9	73.2	74.5	76.6	77.1
	Corn	23.7	2.3	18.9	19.7	22.2	23.8	25.3	27.3	28.0
	Deer	0.7	0.7	0.0	0.0	0.2	0.5	1.1	2.0	2.4
	Human Food	2.4	2.0	0.1	0.2	0.9	1.9	3.3	6.3	7.4
					Model 22					
Nuisance	C_3 Plants	69.9	8.9	48.9	53.5	64.5	70.7	76.1	82.7	84.7
	Corn	19.1	7.1	5.9	7.7	14.0	19.0	23.7	31.2	33.3
	Deer	2.4	4.0	0.0	0.0	0.2	0.9	2.7	9.7	14.6
	Human Food	8.7	10.4	0.0	0.1	1.2	4.5	12.2	31.9	38.5
Non-nuisance	C_3 Plants	78.8	4.7	69.4	71.2	75.5	78.7	82.0	86.7	88.0
	Corn	16.9	4.7	7.9	9.3	13.6	16.9	20.3	24.5	26.0
	Deer	1.1	1.3	0.0	0.0	0.3	0.7	1.5	3.7	4.8
	Human Food	3.2	3.0	0.1	0.2	1.0	2.3	4.5	9.1	10.7
Oak: Excellent	C_3 Plants	78.8	4.7	69.4	71.2	75.5	78.7	82.0	86.7	88.0
	Corn	16.9	4.7	7.9	9.3	13.6	16.9	20.3	24.5	26.0
	Deer	1.1	1.3	0.0	0.0	0.3	0.7	1.5	3.7	4.8
	Human Food	3.2	3.0	0.1	0.2	1.0	2.3	4.5	9.1	10.7
Oak: Good	C_3 Plants	72.1	2.4	67.6	68.2	70.5	72.1	73.6	76.0	76.9
	Corn	25.9	2.6	20.5	21.4	24.2	26.0	27.7	29.9	30.6
	Deer	0.5	0.6	0.0	0.0	0.1	0.3	0.7	1.7	2.3
	Human Food	1.5	0.0	0.4	1.0	0.1	2.1	4.4	5.3	0.0
Oak: Poor	C_3 Plants	73.3	2.8	67.8	68.6	71.4	73.2	75.1	77.9	78.9
	Corn	22.4	3.7	14.3	15.9	20.2	22.6	24.9	27.9	28.9
	Deer	0.9	1.1	0.0	0.0	0.2	0.5	1.3	3.1	4.0
	Human Food	3.4	3.3	0.0	0.1	0.9	2.4	5.1	10.2	12.0
					Model 31					
Nuisance	C_3 Plants	65.1	5.8	53.4	55.6	61.4	65.4	69.1	74.1	75.5
	Corn	27.4	6.1	14.5	16.9	23.4	27.8	31.7	36.9	38.8
	Deer	1.9	3.1	0.0	0.0	0.2	0.7	2.3	7.8	10.7
	Human Food	5.5	6.7	0.1	0.1	0.8	2.8	7.9	19.6	24.5
Non-nuisance	C_3 Plants	73.6	3.0	68.0	68.8	71.5	73.5	75.6	78.7	80.0
	Corn	22.9	3.4	16.0	17.1	20.7	23.1	25.2	28.1	29.1
	Deer	0.9	0.9	0.0	0.0	0.3	0.7	1.3	2.8	3.4
	Human Food	2.6	2.3	0.1	0.2	0.9	2.0	3.7	7.2	8.6

Covariate Level	Food Source	Mean	SD	2.50%	5%	25%	50%	75%	95%	97.50%
Male	C_3 Plants	73.4	2.2	69.2	69.8	71.9	73.4	74.9	77.0	77.9
	Corn	24.1	2.6	18.7	19.7	22.5	24.2	25.9	28.0	28.7
	Deer	0.6	0.6	0.0	0.0	0.1	0.4	0.8	1.8	2.4
	Human Food	1.9	2.0	0.0	0.1	0.5	1.3	2.8	5.9	7.1
Female	C_3 Plants	73.6	3.0	68.0	68.8	71.5	73.5	75.6	78.7	80.0
	Corn	22.9	3.4	16.0	17.1	20.7	23.1	25.2	28.1	29.1
	Deer	0.9	0.9	0.0	0.0	0.3	0.7	1.3	2.8	3.4
	Human Food	2.6	2.3	0.1	0.2	0.9	2.0	3.7	7.2	8.6
Model 33										
Nuisance	C_3 Plants	64.0	5.0	54.4	56.0	60.6	63.9	67.3	72.3	73.8
	Corn	29.3	6.3	15.1	17.6	25.7	29.8	33.6	38.5	40.0
	Deer	1.4	2.3	0.0	0.0	0.2	0.6	1.7	5.8	7.3
	Human Food	5.3	6.1	0.1	0.1	0.8	2.9	7.6	18.3	22.4
Non-nuisance	C_3 Plants	71.7	2.6	66.9	67.4	69.9	71.7	73.4	75.9	76.8
	Corn	25.3	2.9	19.5	20.4	23.5	25.4	27.2	29.7	30.6
	Deer	0.7	0.7	0.0	0.0	0.2	0.5	1.1	2.2	2.7
	Human Food	2.3	2.0	0.1	0.2	0.8	1.8	3.2	6.3	7.3
Beech: Excellent	C_3 Plants	71.7	2.6	66.9	67.4	69.9	71.7	73.4	75.9	76.8
	Corn	25.3	2.9	19.5	20.4	23.5	25.4	27.2	29.7	30.6
	Deer	0.7	0.7	0.0	0.0	0.2	0.5	1.1	2.2	2.7
	Human Food	2.3	2.0	0.1	0.2	0.8	1.8	3.2	6.3	7.3
Beech: Fair	C_3 Plants	74.1	4.1	66.3	67.4	71.3	74.1	76.8	80.9	82.2
	Corn	21.5	4.8	11.2	12.9	18.5	21.8	24.8	28.7	30.2
	Deer	1.0	1.4	0.0	0.0	0.1	0.5	1.2	3.7	4.7
	Human Food	3.4	3.9	0.0	0.1	0.7	2.1	4.7	11.9	14.7
Beech: Poor	C_3 Plants	75.1	2.8	70.0	70.7	73.1	75.0	76.9	79.9	80.9
	Corn	22.4	3.2	15.6	16.7	20.5	22.6	24.5	27.2	27.8
	Deer	0.6	0.8	0.0	0.0	0.1	0.3	0.8	2.1	2.8
	Human Food	2.0	2.2	0.0	0.1	0.4	1.2	2.7	6.5	8.1

5.2 Appendix B: Figures

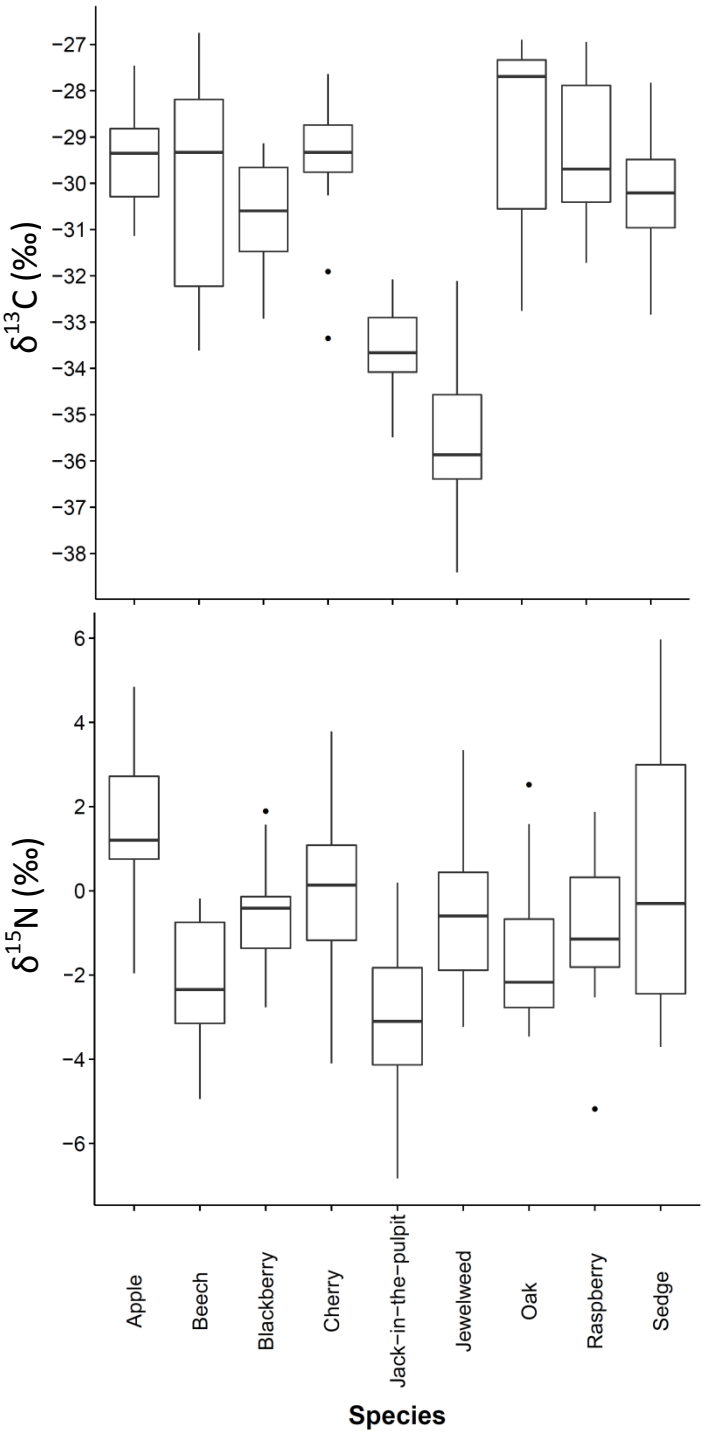

Figure A-5.1. Boxplots showing the difference in carbon and nitrogen isotope values between C_3 plant species that are part of black bear diet in Vermont. Upper and lower hinges correspond to 25th and 75th percentiles, centerline represents the median, and whiskers extend to the highest and lowest values within 1.5 * Inter-quartile range. Values beyond these limits are represented by outlier dots.

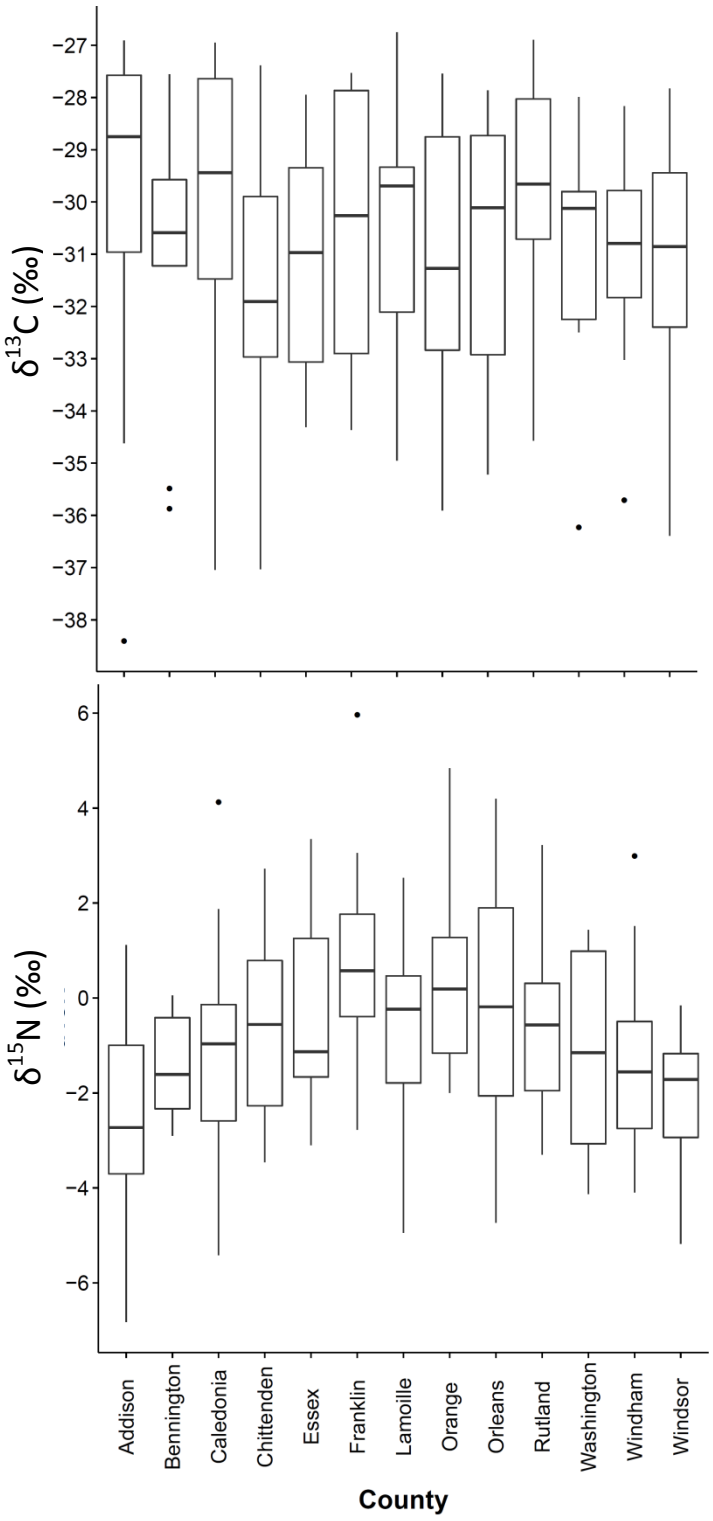

Figure A-5.2. Boxplots showing the difference in $\delta^{13}C$ and $\delta^{15}N$ values between C_3 plants, in black bear diet, from different counties in Vermont. Upper and lower hinges correspond to 25th and 75th percentiles, centerline represents the median, and whiskers extend to the highest and lowest values within 1.5 * Inter-quartile range. Values beyond these limits are represented by outlier dots.

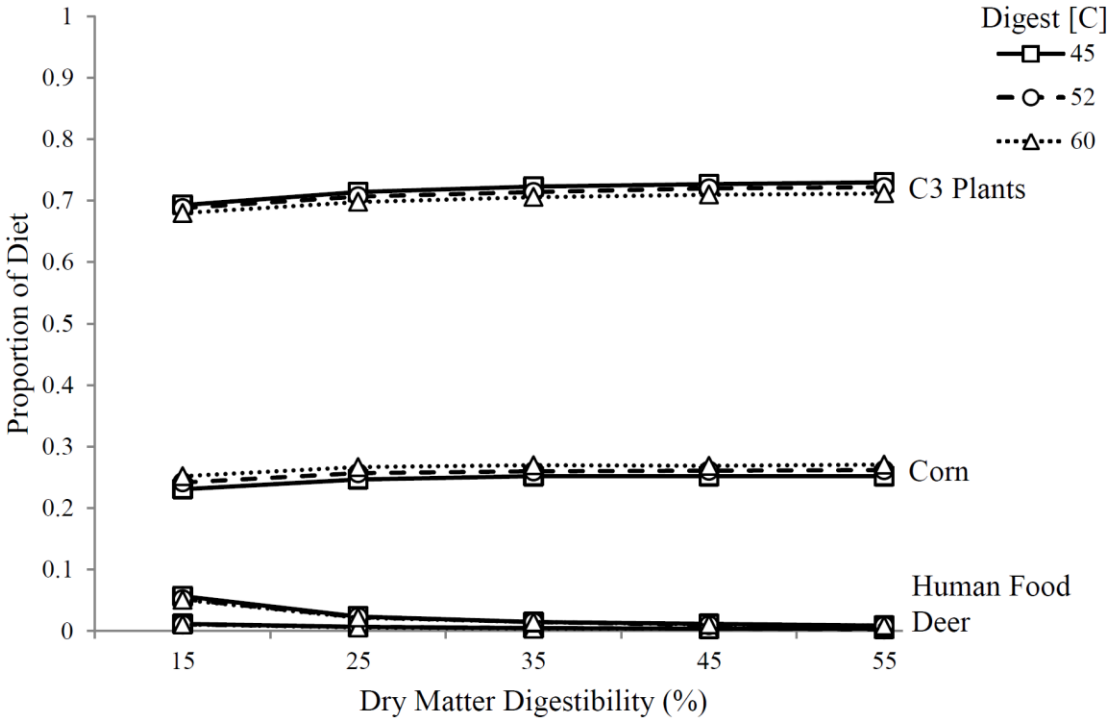

Figure A-5.3. Results of a sensitivity analysis that altered dry matter digestibility and the [C] of digested dry matter for leafy plants within the C_3 plant group. Effects on estimated proportions of food groups are shown.

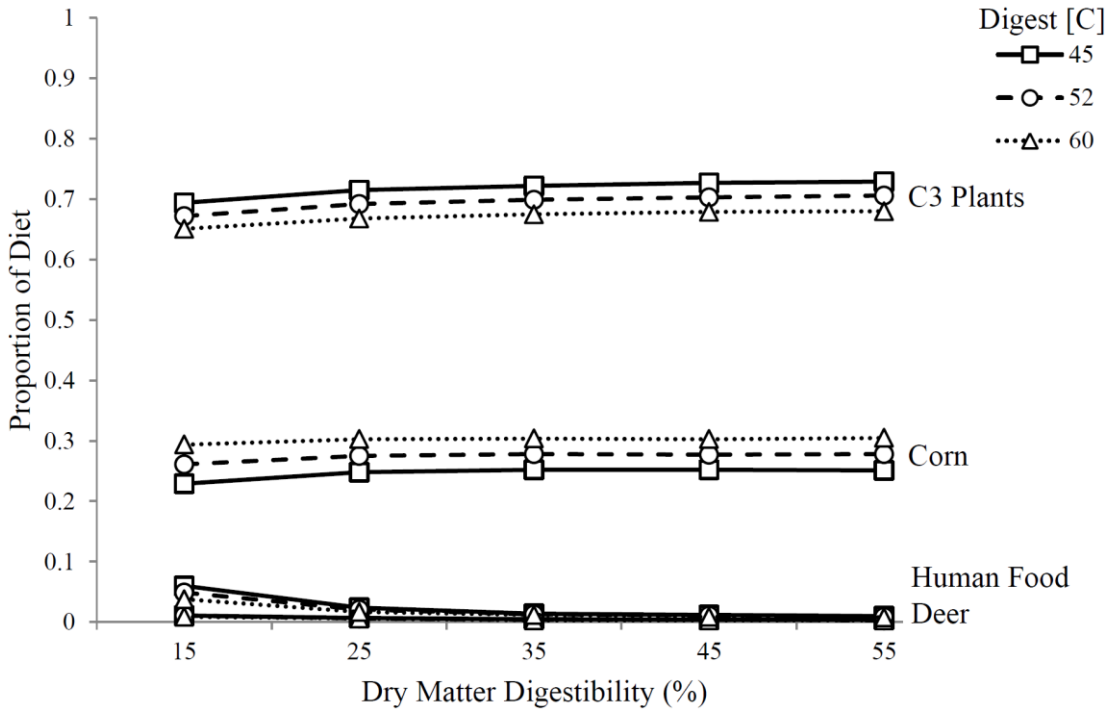

Figure A-5.4. Results of a sensitivity analysis that altered dry matter digestibility for leafy plants and the [C] of digested dry matter for all plants within the C_3 plant group. Effects on estimated proportions of food groups are shown.

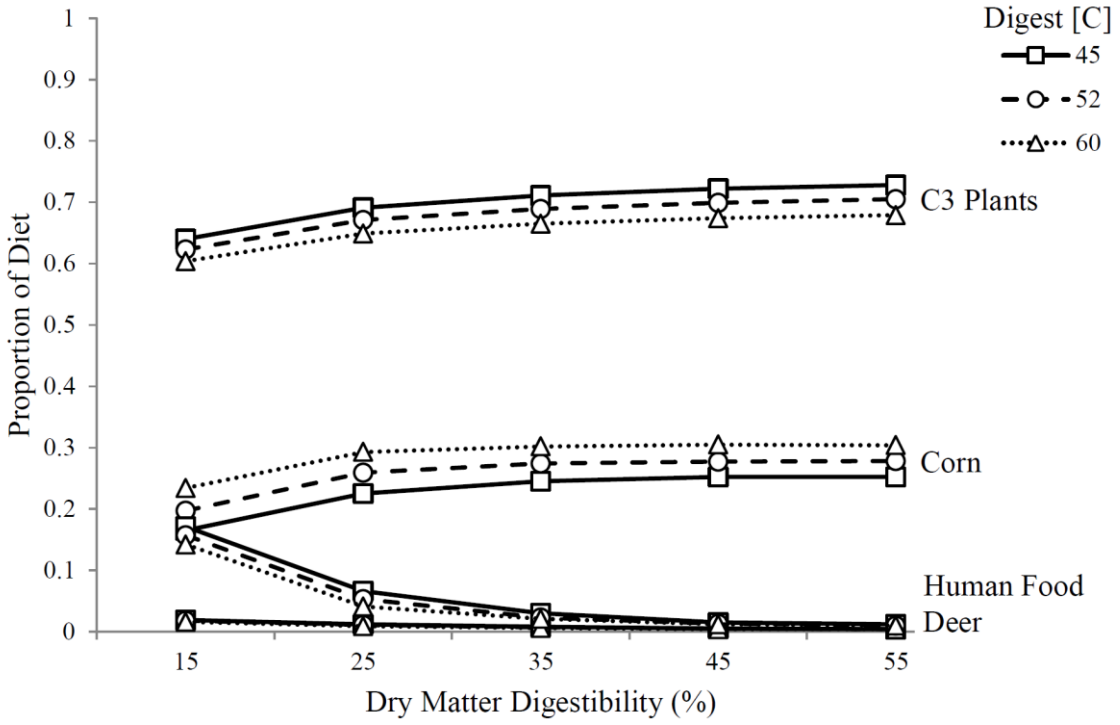

Figure A-5.5. Results of a sensitivity analysis that altered dry matter digestibility and the [C] of digested dry matter for all plants within the C_3 plant group. Effects on estimated proportions of food groups are shown.

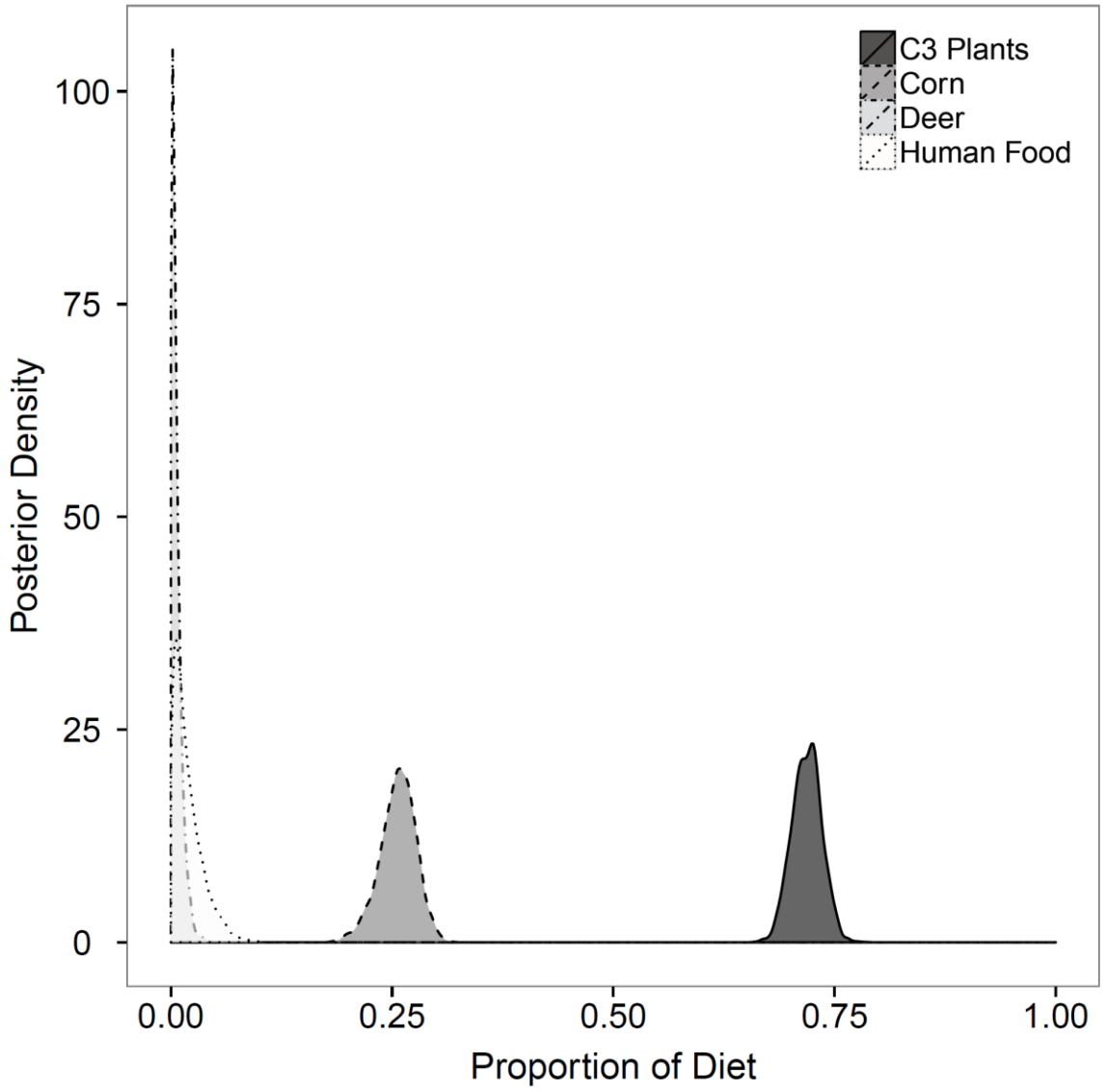

Figure A-5.6. Overall posterior density estimates of diet source contributions to black bears killed in Vermont resulting from Model 1 (null without covariates). This model used digestibility incorporated concentration dependence values and both residual and process error.

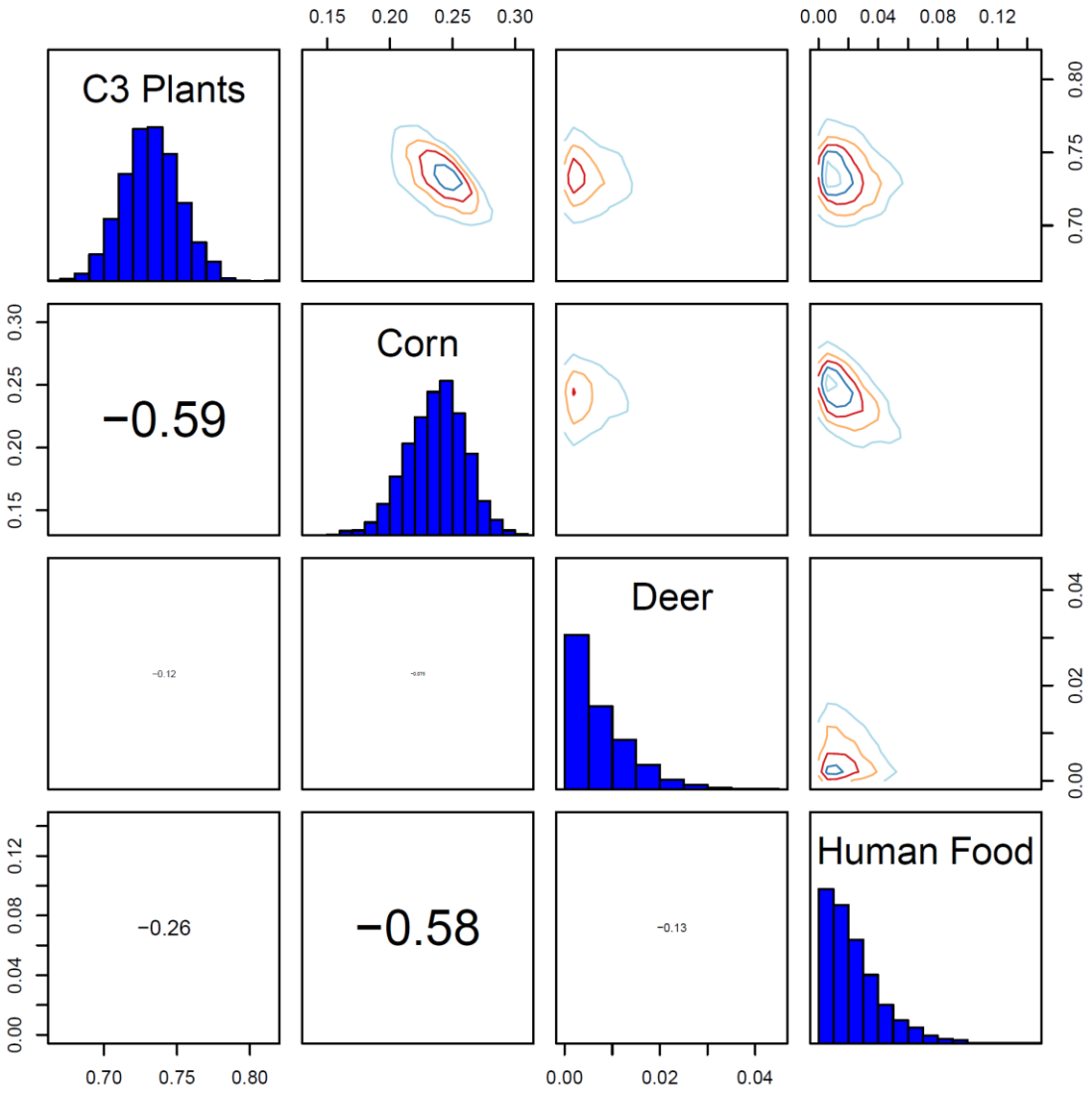

Figure A-5.7. Matrix plot of food sources for the covariate model with the lowest DIC score (Model 17). The diagonal cells show the posterior probability distribution for each of the four potential food sources. The cells below diagonal histograms show the correlations between contributions for each pair of food sources. Cells above diagonal histograms show contours of joint posterior probability distributions for pairs of food sources and their contributions.